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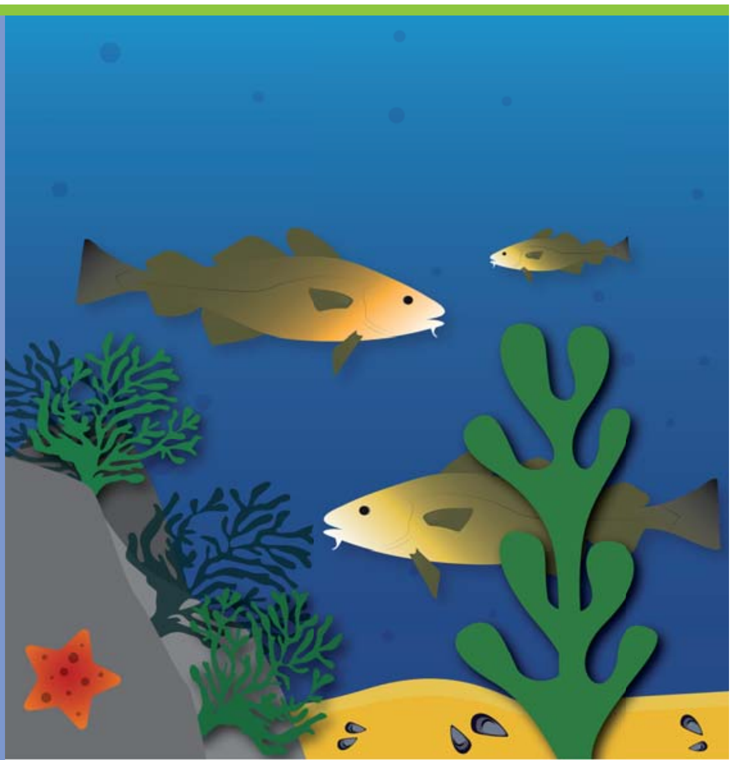
PhD Thesis



Written by Louise Dahl Kristensen
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DTU Aqua
National Institute of Aquatic Resources

The importance of habitat structure for the distribution and behaviour of demersal fish

Louise Dahl Kristensen

PhD Thesis

2016

Technical University of Denmark

National Institute of Aquatic Resources

Section for Ecosystem based Marine Management

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Front page illustration by Søren Kristensen

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PREFACE

This thesis is the result of a three year PhD project at the Technical University of Denmark at the National Institute of Aquatic Resources. The PhD has been completed alongside a part time position as administrative assistant for the Key Fishermen project where volunteer recreational fishermen contributed to the project with their catches from gill nets and fyke nets from fixed locations all over Denmark. In addition, the PhD has been prolonged due to two family additions, the writing of a report on the Key Fishermen project and editing of a report on the effect of stone reefs as nursery and spawning area.

The PhD was carried out at the National Institute of Aquatic Resources, Technical University of Denmark (DTU Aqua) in collaboration with Department of Bioscience - Aquatic Biology at Aarhus University. The research was financed by the European Fishery Fund and the Danish Marine Coastal Fisheries Management Program (Fiskepleje).

Many people are to be thanked for their support and involvement in my PhD project. My greatest gratitude goes to Josianne Støttrup for pushing me to achieve my best and for believing in me from the very beginning. I have learned much from you, and I thank you for the past nine years of our professional collaboration. I am grateful to Claus Stenberg for his advice and encouragement throughout my PhD. I enjoyed the many hours we spent together at sea collecting data. In spite of the long days you were always able to lift the spirit of the crew. And thank you, for always being available for statistical help. I would like to thank Peter Grønkjær for his help and trust in me. You were the familiar face in the tentative beginning of this project and that means more than I can say.

I would also like to thank all the people at DTU Aqua. Stine Kærulf Andersen, Louise K. Poulsen, Helle Torp Christensen and Jesper Knudsen, it was a pleasure working with you and I learned a lot from you all. Thanks also to my office mates Eleonora, Filipa and Elliot, I enjoyed the time we shared in our office. Viola, I hate to finish without you, hurry up! I had not been able to collect my data without volunteering fisherman, Poul Erik Nielsen – I am very thankful for your endurance.

My warmest thanks go to my family and friends, who continuously encouraged and supported me throughout the PhD. You have all been a tremendous help to me. My warmest thanks go to Signe for her support and love through the ups and downs of the PhD – you are my rock! And to my children Laura & Lauritz for always putting things in perspective, making me forget hard times and enjoy the moment.

Louise Dahl Kristensen
Sydhavnen, 1st of April 2016

ENGLISH SUMMARY

This PhD project investigated the effects of coastal habitat structural characteristics on the biodiversity, abundance, size range and behaviour of fish, whilst maintaining a particular focus on the effect of habitat restoration. Fish distribution and behaviour was measured using a combination of gill net sampling, video recordings and acoustic telemetry.

Some biogenic temperate reefs have declined to commercial extinction, in several countries, due to a host of impacts, including overexploitation, parasites and the loss of hard biogenic substrate. The recovery of these reefs may be slow or, without sufficient hard bottom, even impossible. Bivalves are ecosystem engineers as they modify the benthic environment and influence the health of other organisms. Additionally, biogenic reefs provide ecosystem services such as reducing turbidity and improving water quality which make bivalves ideal organisms for consideration in habitat restoration project. In the present thesis, blue mussel (*Mytilus edulis*) beds were established cost-effectively using crowdsourcing and the help of local volunteer fishermen (**Paper I**). A total of 44 tons of blue mussels were produced and established in beds over an area of 121,000 m^2. The effect of the artificial mussel beds was most evident on a small scale resulting in an increased biodiversity and a three times higher abundance of small fish on the introduced mussel structures. To our knowledge, this is the first attempt to use established mussel beds for improving fish habitats and the new method is a potentially useful management tool in areas where mussel spat are abundant.

Globally bottom trawling and dredging reduces the complexity of benthic structures by spreading and flattening marine boulder reefs which results in a reduced abundance and biodiversity of marine species. In addition, boulder reefs have been destroyed through targeted extraction of boulders for the construction of piers and jetties with a presumed high loss of biomass and numbers of hard bottom species. As boulder reefs are unable to restore themselves, they depend entirely on habitat restoration. Therefore, a boulder reef was successfully restored with the addition of 100,000 tons Norwegian quarry boulders deployed on approximately 27,400 m^2 of seabed. The boulders stabilized the existing reef and reintroduced the cave forming reef structures. The restored boulder reef increased the biodiversity and the abundance of reef associated fish such as Atlantic cod (*Gadus morhua*), saithe (*Pollachius virens*) and goldsinny wrasses (*Ctenolabrus rupestris*). Restoration also increased the proportion of larger individuals present, both within species and across the whole fish assemblage (**Paper II**). In addition, the restoration increased the abundance of invertebrates fivefold and the biomass 14-fold (**Paper III**). This increase in food availability was also evident in cod stomach contents, where the biomass increased threefold. Cod stomach contents indicated a shift from a diet based on smaller crustaceans towards high quality food items. Furthermore, using telemetry and acoustically tagged cod, results showed that a larger fraction of the tagged cod remained in the study area with the restored boulder reef compared to before restoration, and with this an increase in residence time was also observed (**Paper IV**). This thesis show unique results from the first ever restored boulder reef and the results are thus highly relevant for future management of degraded hard bottom habitats. Our study indicates that boulder reef restoration could be a valuable management tool to improve habitats for temperate fish species.

DANSK RESUMÉ

Denne ph.d.-afhandling fokuserer på kystnære habitater og deres effekt på biodiversitet, tæthed, størrelsesfordeling og adfærd hos fisk. Nærværende projekt lægger specielt vægt på effekten af habitatrestaurering, og fordelingen af fisk blev undersøgt vha. garnfangster, videooptagelser og akustisk telemetri.

Visse biogene rev er blevet mindre hyppige og er i adskillige lande truet til kommerciel udryddelse pga. overfiskeri, parasitter og tab af egnede hårdbundshabitater, som larverne kan sætte sig fast på. Visse muslingearter kommer sig kun langsomt, og uden et passende hårdt substrat til larverne, kan gendannelsen af biogene rev være umulig. Muslinger formår at ændre miljøet på havbunden, idet muslingeskallerne i sig selv udgør et habitat for andre organismer. Derudover reducerer muslinger uklarheder i vandet og forbedrer vandkvaliteten, hvilket gør dem til ideelle fokusarter i habitat-restaureringsprojekter. I denne ph.d.-afhandling blev blåmuslingebanker (*Mytilus edulis*) etableret kosteffektivt vha. *crowdsourcing* og gennem samarbejde med lokale frivillige fiskere (**Paper I**). I alt blev der produceret 44 tons blåmuslinger, som blev lagt ud i spredte muslingebanker på 121.000m^2. Effekten af de menneskeskabte muslingebanker var tydeligst på helt nært hold, hvor man konstaterede en øget biodiversitet og en tre gange højere tæthed af småfisk sammenlignet med kontrolområdet. Så vidt vides, er nærværende projekt det første forsøg på at bruge menneskeskabte muslingebanker til at forbedre fiskehabitater, og denne nye metode er potentielt et nyttigt værktøj i forvaltningen af marine habitater i områder med muslingeyngel.

I hele verden reducerer bundslæbende redskaber kompleksiteten af stukturer på havbunden f.eks. ved at udjævne de kampesten, der udgør et stenrev, og dermed bliver strukturerne på havbunden fladere og fladere. Derudover har råstofindvinding ødelagt et ukendt antal stenrev i Danmark, for at bruge kampestenene til konstruktion af havnekajer og moler. Dette har formentlig resulteret i et stort tab af biomasse og tætheder af hårdbundslevende arter. Da stenrev ikke er i stand til at gendanne sig selv, afhænger de helt og aldeles af habitatrestaurering. Derfor blev et stenrev restaureret vha. 100.000 tons norske kampesten (udvundet fra et fjeld) udlagt på ca. 27.400m^2 havbund. Kampestenene stabiliserede det eksisterende rev og genskabte de huledannende strukturer. Der var en signifikant stigning i tætheden af torsk (*Gadus morhua*) og sej (*Pollachius virens*), og størrelsesfordelingen steg overordnet set for alle fisk samt specifikt for torsk og berggylt (*Labrus bergylta*) (**Paper II**). Også biodiversiteten steg som følge af restaureringen af revet. Ligeledes steg tætheden af bundlevende invertebrater med en faktor fem og biomassen med en faktor 14 (**Paper III**). Stigningen i fødetilgængelighed var også synlig i maveindholdet hos torsk, hvor biomassen var tre gange så stor efter revrestaureringen. Maveindholdet hos torsk indikerede et diætskifte fra primært at bestå af små krebsdyr til at være domineret af byttedyr af høj fødekvalitet. Endvidere påviste vi vha. telemetri og akustisk mærkede torsk, at en større andel af de udsatte torsk forblev på revet og at torskene tilbragte mere tid på revet efter restaurering (**Paper IV**). Denne afhandling viser enestående resultater fra den første stenrevsrestaurering som er yderst relevante for fremtidig forvaltning af ødelagte hårdbundshabitater. Vores studie indikerer, at restaureringen af stenrev kan være et værdifuldt forvaltningsværktøj til at forbedre levesteder for fisk i kystnære habitater.

LIST OF PAPERS

This PhD thesis is based on the following papers:

Paper I

ESTABLISHMENT OF BLUE MUSSEL BEDS TO ENHANCE FISH HABITATS
KRISTENSEN, L.D., STENBERG, C., STØTTRUP, J.G., POULSEN, L.K., CHRISTENSEN, H.T., DOLMER, P., LANDES, A., RØJBEK, M., THORSEN, S.W., HOLMER, M., DEURS, M.V., GRØNKJÆR, P.
(*Published*)

Paper II

RESTORATION OF A TEMPERATE REEF: EFFECTS ON THE FISH COMMUNITY
STØTTRUP, J.G., STENBERG, C., DAHL, K. KRISTENSEN, L.D., RICHARDSON, K.
(*Published*)

Paper III

ECOLOGICAL EFFECTS OF BOULDER REEF RESTORAION ON PREY ABUNDANCE AND FEEDING BEHAVIOUR OF FISH
KRISTENSEN, L.D., STØTTRUP, J.G., STENBERG, C., DAHL, K., LUNDSTEEN, S., ANDERSEN, O.G.N., GRØNKJÆR, P.
(*Manuscript*)

Paper IV

BEHAVIOURAL CHANGES OF ATLANTIC COD (*GADUS MORHUA*) AFTER BOULDER REEF RESTORTION: IMPLICATIONS FOR COASTAL MANAGEMENT
KRISTENSEN, L.D., STØTTRUP, J.G., SVENDSEN, J.C., STENBERG, C., GRØNKJÆR, P.
(*Manuscript*)

INTRODUCTION

Background

Ecology of coastal habitats

The habitats along the world's coastline are highly varied and range from flat, coastal plains, brackish estuaries, saltmarshes, mangroves, seagrass meadows, macroalgae communities, biogenic reefs, coral reefs and rocky shores. These are all highly productive habitats and they also offer invaluable ecosystem services. The importance of coastal habitats for marine fisheries is increasingly recognized. It is estimated that 44% of all fish and shellfish species that ICES give advice on in the Northeast Atlantic utilize coastal habitats at one or more life stages (Seitz et al. 2014). These species cannot complete their life cycle without coastal habitats, making them essential habitats. Studies show a positive relationship between the size of the nursery area and the size of a fish population (Gibson 1994, Sundblad et al. 2014), suggesting that lack of essential fish habitat is limiting for the population size.

The causes of habitat destruction

It is estimated that the number of people living within 100 km from the coast was 2.2 billion in 1995 (Burke et al. 2001) and in Denmark no one lives more than 50 km from the coast. As the human population increases in coastal areas so does the pressure on coastal ecosystems, and habitat loss due to human impact is one of the greatest threats to marine ecosystems (Wolff 2000, Lotze et al. 2006). In Europe it is estimated that 85% of the European coastlines are degraded (Bryant et al. 1995, EEA 1999). This is particularly disturbing because the temperate regions also are among the most productive ecosystems on Earth (Suchanek 1994). Destructive trawl fisheries have a devastating effect on marine habitats and the effect of mobile fishing gear on the seabed has been likened to forest clearcutting (Watling & Norse 1998). When exposed to repeated trawls, as is common in the Northeast Atlantic, the seabed becomes homogenized with severe effects on the benthic community and thus on sediment stability, water column turbidity and carbon processing (Thrush & Dayton 2002). High nutrient loading and eutrophication has a negative impact on the colonization of benthic vegetation such as seagrasses and macroalgae (Eriksson et al. 1998, Nielsen et al. 2002a, b) and seagrass habitats are lost at a concerningly high rate (Waycott et al. 2009). The loss of these vegetated areas effects important ecosystems services such as protection against coastal erosion and nursery grounds for several commercially important species (Seitz et al. 2014). Another threat to marine habitats is the increased atmospheric carbon dioxide that leads to increasing seawater temperatures and decreasing pH-levels in the oceans. Both have impacts on marine communities e.g. when "warm-water" species gradually replace "cold-water" species (Henderson et al. 2011) and the negative impact on the immune system and calcification of calcifying marine organisms which ultimately lowers their growth, reproduction and survival (Kroeker et al. 2010, Mackenzie et al. 2014).

The definition of habitat restoration

According to Bradshaw (1997), the definition of a *habitat* is "*…the place where organisms live*". Furthermore, *restoration* is "*…to bring back to an original state… or to a healthy or vigorous* *state*". Habitat restoration, thus, refers to the action to bring the place where organisms live back to a healthy state. The ultimate aim should be to restore the whole ecosystem rather than single species, even if emphasis is sometimes placed on a particular component (National Research Council 1992). Ecosystems are not static but rather in a dynamic equilibrium, so when we restore them, we are aiming for a "moving target" (Parker & Pickett 1997). It is therefore important that we restore the function rather than the precise form of a habitat (Bradshaw & Chadwick 1980) and that we keep this in mind when comparing the results of the restoration with reference areas. It should also be emphasized that careful monitoring is key to understanding the effect of restoration (Brumbaugh et al. 2006).

Ecology of biogenic reefs

Bivalves are ecosystem engineers and via their own physical structures, they create biogenic habitats for a variety of benthic organisms. Both the abundance and biodiversity of fauna living within a bivalve reef, increase with the complexity of the reef and patch size (Norling & Kautsky 2007, 2008). The high abundances of prey provide excellent feeding opportunities for predators and promotes both fish growth and diversity (Carbines et al. 2004). Especially smaller fish species such as common goby (*Pomatoschistus microps*), rock goby (*Gobius paganellus*) and butterfish (*Pholis gunnellus*) but also larger fish, like flatfishes, use mussel beds as habitat for either direct foraging, breeding or as nursery area (Jones & Clare 1977). Apart from improving coastal habitats by increasing the complexity (McDermott et al. 2008), mussels offer important ecosystem services such as reducing turbidity and improving water quality (Riemann et al. 1988, Coen et al. 2007, Nielsen & Maar 2007) through filtration of suspended inorganics, phytoplankton and detrital particles. The improved water transparency leads to better light conditions for benthic primary producers, e.g. sea grasses (Newell & Koch 2004), allowing them to spread into deeper areas.

Destruction of biogenic reefs

Biogenic temperate reefs such as European oyster beds (*Ostrea edulis*) have declined to commercial extinction in several countries. This is due to a number of factors including overexploitation, parasites and the loss of hard biogenic substrate, which is itself a form negative feedback, reducing available habitat for larvae to settle on (Wolff 2000, Lotze 2005). Scallop dredging is believed to be one of the most destructive fishing methods in biogenic habitats where recovery of the benthic community was estimated to be >970 days post-fishing (reviewed by Kaiser et al. 2006). Certain bivalve species have even longer recovery periods of approximately 10-50 years (Cranfield et al. 2004, Jackson 2007) and without sufficient hard bottom habitats recovery may be slower or even impossible (Kenchington et al. 2006, 2007). In addition, high nitrogen loading increases the algae production (Richardson & Jørgensen 1996) which again increases the oxygen consumption on the seafloor when the microalgae decompose (Glibert et al. 2005). This ultimately leads to periodically oxygen depletion (hypoxia) events (Krause-Jensen et al. 2011, 2012) which leads to mass mortality of the benthic fauna (Jørgensen 1980).

Restoration of biogenic reefs

Due to the slow recovery of biogenic reefs, they may in some cases benefit from habitat restoration to speed up the recovery process. Numerous attempts have been made to restore American oyster reefs (*Crassostrea virginica*). Studies have shown that even three years after establishment of the reef, oyster densities were still only 17-23% of the densities in adjacent natural reefs, but the biodiversity was similar on established and natural oyster reefs (Coen & Luckenbach 2000). It has been estimated that 10 m^2 of restored oyster reefs can produce 2.6 kg of fish and large mobile crustacean each year (Peterson et al. 2003). As the function of biogenic reefs is more important than the species comprising the structure (Palomo et al., 2007; Norling and Kautsky, 2007), it is expected that establishment of mussel beds could, in a manner similar to oyster beds, improve fish habitats.

The biogenic study site

The seabed in Nørrefjord near Faaborg, Denmark (**Fig. 1**), was previously dominated by blue mussel beds (Rask et al. 2000) but hypoxia events following eutrophication is believed to have degraded the benthic habitats with an associated decline in fish populations. Furthermore, the fjord has experienced extraction of sand and gravel from 1950-1990 (Personal observation, Niels Christian Christensen, local fisherman) which reduces the complexity of the bottom and the habitat quality (Nielsen & Petersen 2013). This general deterioration of the fjord is of great concern to the local recreational fishermen, who experience declining fish catches. The recreational fishermen therefore initiated the present project to improve conditions for fish by promoting fish habitats in Nørrefjord. This project is unique through the close collaboration between local stakeholders, local managers and researchers. To our knowledge, this is the first attempt to restore or establish a blue mussel bed with the primary objective to enhance fish habitats, and the results are thus important for national as well as international biogenic reefs restoration.

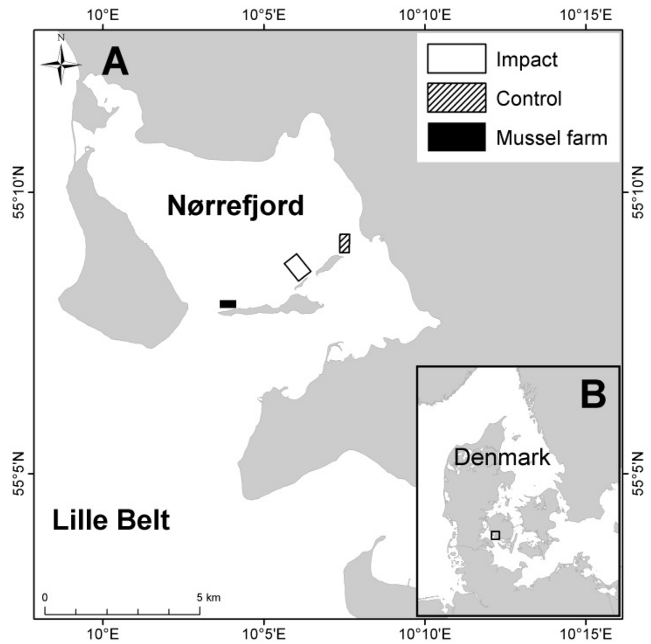

Figure 1. Study area. A) Location of the mussel farm, the Impact area, and the Control area. B) Location of Nørrefjord in Denmark

Ecology of boulder reefs

Hard bottom habitats are identified as essential fish habitats because several species utilize these habitats at one or more life stages. In reality very few studies have focused on the importance of hard bottom habitats, but we do know that a number of economically and ecologically important species such as herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*) and European eel (*Anguilla anguilla*) utilize hard bottom habitats for spawning, feeding, and/or as a nursery (Blegvad 1916, Rajasilta et al. 1989, Norderhaug et al. 2005, reviewed by Seitz et al. 2014) (**Table 1**). The primary reason why hard bottom habitats are so important is that they provide substrate for vegetation. These vegetated areas are highly productive and offer shelter for myriads of prey organisms such as amphipods and gastropods. Studies on temperate kelp forests have revealed average fauna densities exceeding half a million animals per m^2 with up to 90,000 specimens on a single kelp (Christie et al. 2009). The vegetation thus offers good feeding opportunities for predators.

Destruction of boulder reefs

Bottom trawling and dredging reduces the complexity of benthic structures by spreading and flattening marine boulder reefs resulting in a reduced abundance and biodiversity of marine species (Thrush & Dayton 2002, Gray et al. 2006). Studies on the effect of mobile fishing gear on hard bottom habitats are reported globally e.g. from the UK, Faroe-Shetland Channel and Alaska (Freese et al. 1999, Gordon 2002, Gage et al. 2005). In addition, boulder reefs have been destroyed through targeted extraction of boulders for the construction of piers and jetties. In Denmark, boulders are a limited resource and the extraction of boulders for the construction industry were carried out for over a century until it was finally banned in 2010 (Nature Protection Act, *LBK nr. 950, 24th of September 2009*). In comparison Germany had already banned stone fishing in 1974 (Bock et al. 2004). It is unknown where and how many reefs were destroyed by this activity, but a rough estimate is that 40 km^2 of the approximately 1200 km^2 known stone reefs in Danish territory were removed from 1950-2000 (Dahl et al. 2003). Anecdotal evidence from the stone fishermen suggests that most of the stone fishing occurred in shallow areas where the stones were more easily accessible. Boulder extraction is believed to have destroyed many coastal boulder reefs with a presumed high loss of biomass and numbers of hard bottom species (Vogt & Schramm 1991, Dahl et al. 2003) and having a large effect on the population structure of fish utilizing hard bottom habitats (Seitz et al. 2014, Sundblad et al. 2014).

Restoration of boulder reefs

Temperate boulder reefs are included in the EU Habitats Directive which obliges us to protect and if necessary restore these important habitats. As boulder reefs are unable to restore themselves, they depend entirely on habitat restoration. To the author’s knowledge at the time of publication, no boulder reef has previously been restored anywhere. One explanation for this is that boulders may not be as scarce a resource in other countries as they are in Denmark. Only one project has “reconstructed” boulder reefs and investigated the effect of limestone boulders embedded in a concrete matrix and an artificial reef constructed of limestone boulder stacked to form caves (Dupont 2008). However, as the study area was previously devoid of structural relief, this is not a "restoration" of a boulder reef *per se*. Instead the project can be viewed as a compensatory mitigation for the loss or degradation of hard bottom habitats caused by a pipeline construction or perhaps even a restoration of the function or ecology of the degraded habitats.

Table 1. Commercially and ecologically important fish and invertebrate species utilizing hard bottom habitat. Modified after Seitz et al. (2014).

Species	English name	Spawning	Nursery	Foraging	Migration	Reference
Anguilla anguilla	European eel		x	x		Blegvad 1916, Moriarty & Dekker 1997, Pihl & Wennhage 2002, Bergström et al. 2011
Clupea harengus	herring	x				Pihl & Wennhage 2002, Rajasilta et al. 1989
Gadus morhua	Atlantic cod		x			Pihl & Wennhage 2002, Norderhaug et al. 2005
Pollachius pollachius	pollack		x			Pihl and Wennhage 2002, Norderhaug et al. 2005
Pollachius virens	saithe		x			Pihl and Wennhage 2002, Norderhaug et al. 2005
Salmo salar	salmon				x	McCormick et al. 1998
Salmo trutta	trout			x		Pihl & Wennhage 2002
Homarus gammarus	European lobster		x	x		Howard & Bennett 1979, Jensen et al. 1994, Wahle & Steneck 1991
Cancer pagurus	edible crab		x	x		Thrush 1986, Hall et al. 1993, Sheehy and Prior 2008
Mytilus edulis	blue mussel	x	x	x		Lintas and Seed 1994, Prins and Smaal 1994, Walter and Liebezeit 2003

The boulder reef study site

Læsø Trindel in Kattegat, Denmark (**Fig. 2**), was one of the many reefs where boulders were extracted for the construction industry (Dahl et al. 2003). Historical maps of the area showed that the shallowest part of the reef gradually increased from 1.25 m in 1831 to ~4 m in the 1970s (Stenberg et al. 2015). It is unknown how many boulders were mined from this reef complex, but in order to restore to the former depth range, approximately 100,000 m^3 boulders was required. In 1991 the site was included in the National Marine Monitoring Program and became a NATURA 2000 site (The Danish Nature Agency 2013). Based on the results from the monitoring, it was concluded that the extraction of boulders had destabilized the reef and the status of the reef was not satisfactory because of the large proportion of opportunistic species (Dahl et al. 2009, Fredshavn et al. 2014). In some cases, the attached macroalgae functioned as a "sail" during periods of high physical stress, dragging the stones with vegetation into the deeper areas leaving the algae to decompose and creating hypoxic bottom conditions. To improve the conditions at Læsø Trindel to meet the criteria of the Habitats Directive, the boulder reef required a restoration. This restoration project is, to the author's knowledge at the time of publication, the first attempt to restore a temperate boulder reef, and the results are thus important for the management of reefs in Danish waters as well as the further development of boulder restoration internationally.

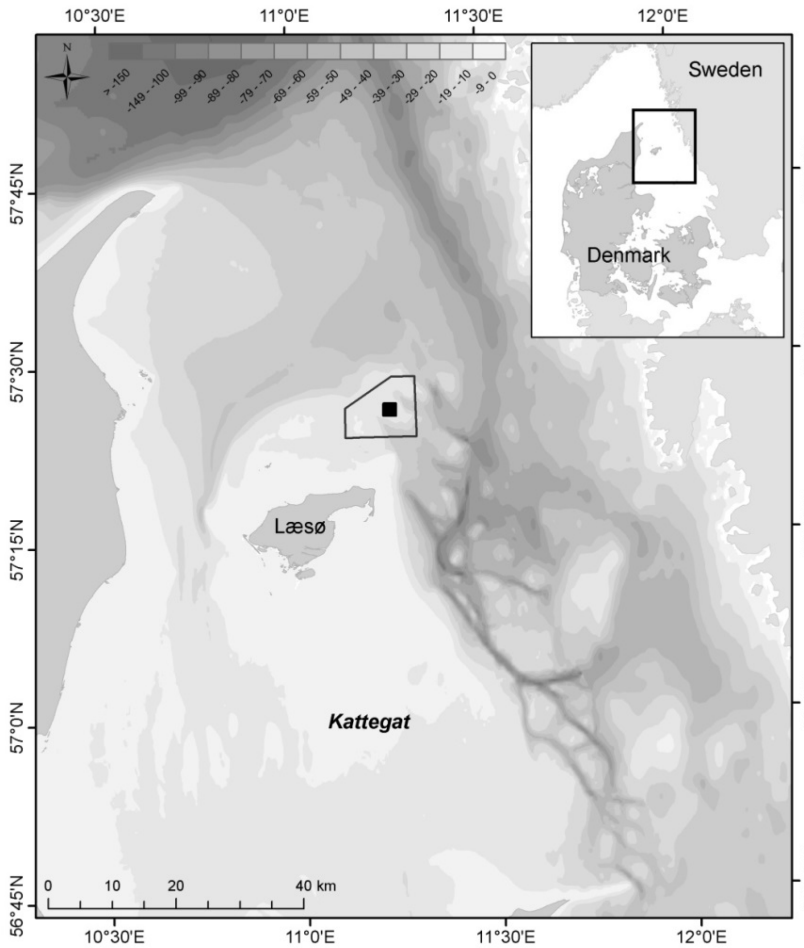

Figure 2. The boulder reef Læsø Trindel (black square) within the NATURA 2000 site no. 168 "Læsø Trindel and Tønneberg Banke" (black outline) in Kattegat between Denmark and Sweden.

Aim and objective

In context of the above, the present PhD project had five aims:

1. To test if restoration or establishment of physical complexity and structure was possible and if so, would it lead to:
2. An increase in the diversity of fish species.
3. An increase in the abundance of individual fish.
4. An increase in the size range of fish.
5. A change in cod behavior measured via increased stomach content and residence time.

This PhD project investigated the effects of coastal habitat's structural characteristics on the distribution of fish, whilst maintaining a particular focus on the effect of habitat restoration. Fish distribution and behaviour was measured using a combination of gill net sampling, video recordings and acoustic telemetry.

To test the aforementioned hypotheses, biogenic reefs were established in a Danish Fjord (Nørrefjord). When establishing cultured mussels, it is standard procedure to dredge natural bottom mussels for seeds and then transplant the mussels to a different area from a specialized vessel (Dolmer et al. 2012). Neither the destructive dredging nor the use of expensive machinery was repeated in the present study. This PhD project instead tested new methods of blue mussel production and establishment of mussel bed using crowdsourcing. With the help of volunteer local fishermen, we conducted the experiment cost-effectively (**Paper I**). The restoration project involved testing of two new methodologies for the local production of blue mussels (*Mytilus edulis*) using suspended long lines or hemp sacks. The effect of habitat restoration also included analysis of eel grass (*Zostera marina*), secchi depth, benthic communities and fish distribution.

In addition, the effect of a boulder reef restoration was tested on the restored Blue Reef at Læsø Trindel. Læsø Trindel was restored in 2008 and the sampling of the *Before*-scenario was carried out in 2007 (Stenberg et al. 2015). This PhD involved sampling of the *After*-scenario in 2012 and the analysis and discussion of the results. The focus of **Paper II** was on the restoration effect on fish diversity, abundance and mean length before and after restoration. **Paper III** evaluated the effect of restoration on prey abundance and changes in the diet of Atlantic cod and goldsinny wrasse (*Ctenolabrus rupestris*). Furthermore, ecological changes on the reef were analysed by dividing the prey organisms into groups according to substrate association and taxonomy (**Paper III**). Very few studies have evaluated the success of restoration projects through animal behaviour, however, the habitat use and residency of a few key species may be more important and cost-effective than to document the distribution of all species (Lindell 2008). Therefore the focus of **Paper IV** was on the effect of boulder reef restoration on Atlantic cod behaviour and residence time.

Outline

This thesis gives an overview of the importance of habitat structures for the distribution and behaviour of fish with special emphasis on habitat restoration. The following chapter encompasses the effect of habitat structures on diversity, abundance, growth, animal body-size and predator-prey interactions with main focus on marine fishes. Additionally, the method and monitoring of habitat restoration is discussed and future perspectives are considered. Finally, the results are briefly summarized and conclusions of this PhD are drawn.

THE IMPORTANCE OF HABITAT STRUCTURE FOR FISH

The present chapter encompasses the effect of habitat structures on biodiversity, abundance, growth, animal body-size and predator-prey interactions with a focus on marine fishes. The paragraph on biodiversity and abundance is divided into the effects of biogenic reefs and boulder reefs. Only very few studies, if any, have focused on the effects of biogenic reefs on growth, animal body-size and predator-prey interactions, and these paragraphs are thus discussed jointly with boulder reefs. Furthermore, there is an ongoing debate over whether the increase in biomass on artificial or restored structures is a result of simple attraction to the structures or new production (Pickering & Whitmarsh 1997). This is outside the scope of this thesis and the question will thus not be addressed here.

Effect of habitat structure on biodiversity and abundance

Habitat structure is important for the distribution of organisms, and the majority of studies conducted on the topic demonstrate a positive correlation between habitat complexity and biodiversity (Risk 1972, Luckhurst & Luckhurst 1978, reviewed by Tews et al. 2004, Kostylev et al. 2005). The substrate type determines which flora and fauna establish themselves in the area. Structure, such as that created by biogenic reefs, vegetation and boulders, offer different microhabitats where a diverse fauna can establish (Eklöv 1997, Ferreira et al. 2001, Airoldi et al. 2008).

Biodiversity and abundance in biogenic reefs

Bivalve aggregations comprise microhabitats for a wide variety of organisms as they increase the complexity of the benthic environment increasing the opportunity for both shelter and food. The biodiversity and abundance of benthic species are positively correlated to the complexity of the biogenic reefs (Seed 1996, Norling & Kautsky 2007, 2008, Hernández-Ávila et al. 2012; **Paper I**). This complexity can be quantified via the density and patch size of the mussel beds. In addition to structural complexity, factors such as depth and size of the individual mussels also influence which invertebrate species are represented in the bivalve matrix (O'Connor & Crowe 2007, Koivisto & Westerbom 2012). Generally, the most abundant taxonomical groups living within a mussel bed are the Nematoda, Oligochaeta, Amphipoda and Isopoda (Svane & Setyobudiandi 1996, O'Connor & Crowe 2007). These invertebrates comprise good prey items especially for smaller fish such as common goby (*Pomatoschistus microps*), rock goby (*Gobius paganellus*) and black goby (*Gobius niger*) which are found in high abundances on mussel beds (Jones & Clare 1977; **Paper I**). But also larger fish such as flatfishes, cod (*Gadus morhua*), trout/salmon (*Salmo trutta/salar*), eelpout (*Zoarces viviparus*) and butterfish (*Pholis gunnellus*) are attracted by the high abundances of prey that mussel beds provide (Jones & Clare 1977, Carbines et al. 2004; **Paper I**). The importance of biogenic reefs for economically and ecologically important species remains unknown and requires further studies. However, based on the biodiversity and abundance of fauna on biogenic reefs, they may prove to be important in a benthic habitat that is increasingly homogenized and flattened by mobile fishing gear.

Biodiversity and abundance in boulder reefs

Boulder reefs are one of the most structurally complex marine habitats. The boulders themselves comprise high relief, but they also offer holdfast for macroalgae which further increases the structural complexity of the boulder reefs. This is reflected in the abundances, biomass and number of taxonomical groups present on rocky bottoms (Stål et al. 2007). The average abundance of benthic macrofauna was on average three times higher compared to soft bottoms (**Fig. 3a, b, c**). Biomass and mean number of taxa was also approximately twice as high on rocky compared to soft bottoms. When comparing the results of Stål et al. (2007) to those obtained in the present thesis (**Fig. 3d, Paper III**), the mean abundance of macrofauna on Blue Reef prior to restoration was comparable to those obtained on soft bottom by Stål et al. (2007). The relatively low densities

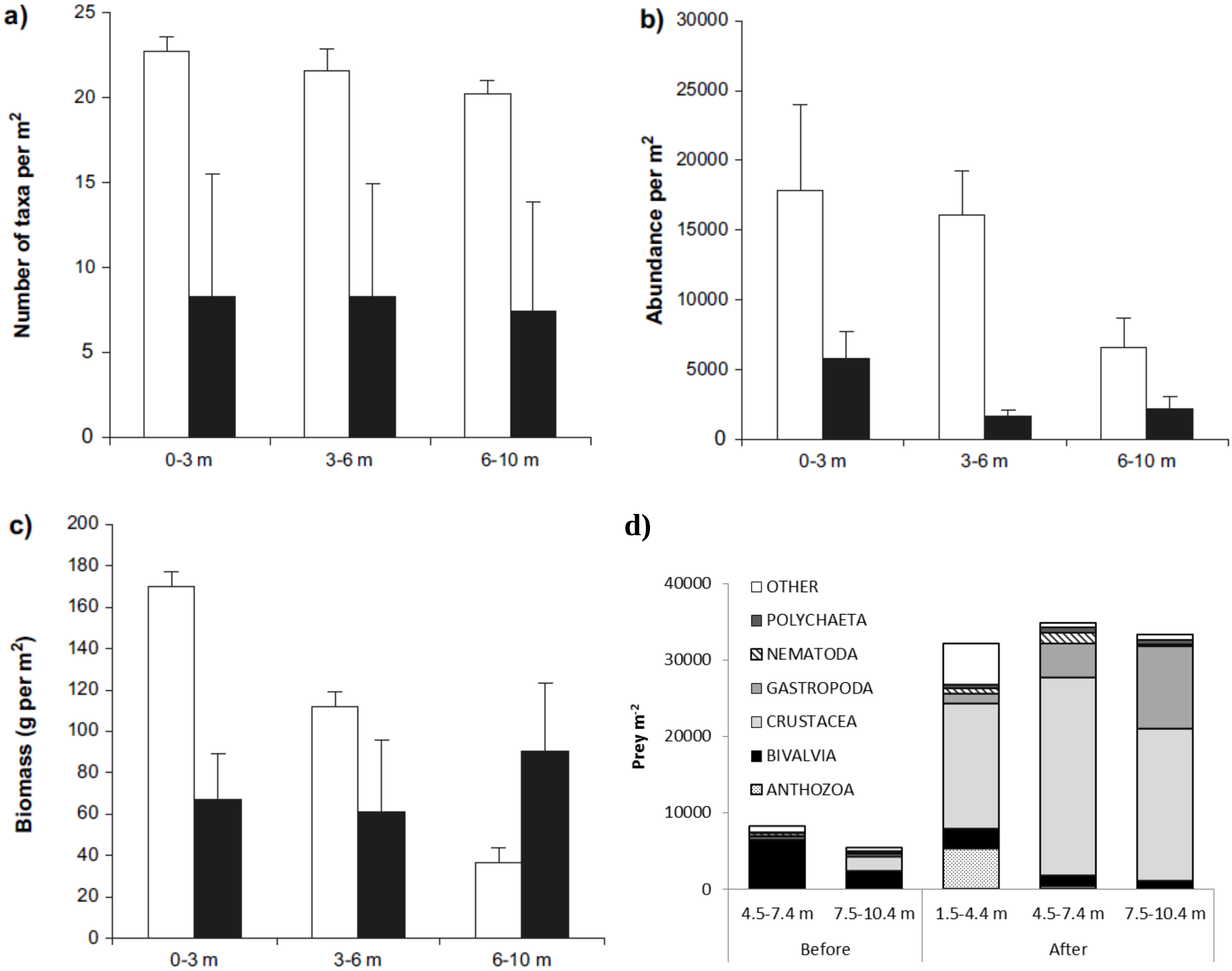

Figure 3. Variation in depth of the substrate associated prey assemblage. (a) number of species, (b) abundance and (c) biomass on rocky (□) and soft bottoms (■) from Stål et al. 2007. (d) abundance of substrate associated prey before and four years after restoration of a temperate boulder reef (**Paper III**).

reflect the poor habitat quality prior to restoration of the reef. The restoration of Blue Reef increased the mean macrofauna density to 31,500 individuals per m^2 – an increase by a factor five. This is a little higher than the densities shown by Stål et al. (2007) on rocky bottoms but lower than densities on other Danish boulder reefs (Dahl et al. 2005, 2016). However, the reef studied in Stål et al. (2007) might be more comparable to Blue Reef based on proximity (Skagerrak, within 100 km) and the level of exposure. These comparisons with Stål et al. (2007) are particularly relevant as the same sampling techniques were applied, i.e. a "suction sampler" (**Fig. 4**) with a 1 mm sieve (Thomasson & Tunberg 2005).

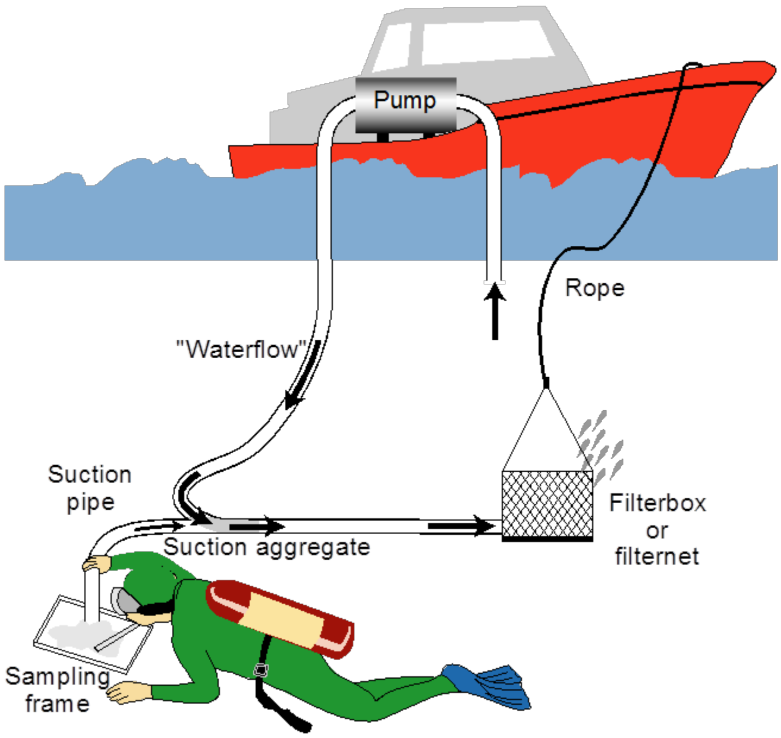

Figure 4. Diver collecting benthic organisms with the suction sampler. Illustration by Britta Munter from Stenberg et al. 2015. Republished with permission from Karsten Dahl.

The primary reason for the increase in macrofauna abundance observed on Blue Reef (**Paper III**) was probably the stabilization of the boulders and thus an increase in the proportion of perennial algae growing on the reef. Studies have shown that fast-growing ephemeral turf algae have the lowest faunal density and even affect fish densities negatively (Pihl et al. 1994, Christie et al. 2009). Diver observations on Blue Reef (**Paper III**) confirmed that the ecological succession was still evolving at the time of the last sampling. The most productive vegetated hard bottom areas were found in Norway where certain temperate kelp forests contain more than half a million individuals per m^2 and one kelp plant up to 90.000 individuals (Christie et al 2009). Further studies on the restored Blue Reef are important to reveal if these restoration efforts are closer to achieving those densities.

Boulder reefs offer feeding and shelter for a great variety of invertebrates and fish. However, the importance of temperate boulder reefs for ecologically and economically important species is largely unknown. Although one study has attempted to address the issue (Stenberg & Kristensen 2015), it is a subject that requires further studies. Based on the biodiversity and abundance of fauna on boulder reefs, they are expected to be of great importance to e.g. cod.

Conclusion on the effect of habitat structure on biodiversity and abundance

This thesis shows that biodiversity and abundance can be increased through an increase of structurally complexity to the benthic environment (**Paper I, II, III, IV**). Both biogenic reefs and boulder reefs comprise physical structures where fauna can seek shelter from predators and forage. As boulder reefs are structurally more complex compared to biogenic reefs, it is not surprising, that the increase in abundance and biodiversity was most pronounced in the study of the boulder reef restoration (**Paper II, III, IV**). Both habitat types offer important ecosystem services such as protection of the coastal area through sedimentation and stabilize the sediment. Biogenic reefs improve the water quality through filtration and thus increase the visibility of the water (Riemann et al. 1988, Nielsen & Maar 2007). Bivalve filtration thus reduces the fallout of e.g. microalgae to the seafloor and thereby reducing the oxygen consumption on the seafloor and lowering the risk of oxygen depletion. Boulder reefs cause turbulence in the water masses (Godoy et al. 2002) and in the photic zone boulders are holdfasts for vegetation. The combination of turbulence mixing the water masses and the oxygen production of macroalgae ultimately reduce the risk of oxygen depletion events in the area. Thus, both habitats improve the water quality and offer important ecosystem services, albeit via different methods.

Effect of habitat structure on growth and animal body-size

Effect on growth

Habitat structure provides shelter from physical stress by reducing the current and providing areas of calm water. Cod have been observed to increase in abundance and seek shelter on the leeward side of structures such as ship wrecks and offshore wind farms (Karlsen 2011, Bergström et al. 2013, Reubens et al. 2014). This shelter seeking behaviour is probably related to energy optimization. The results from studies on Chinook salmon (*Oncorhynchus tshawytscha*) reared in cages with or without vegetation support this theory. The vegetation greatly reduced the velocity of the current and the fish reared in vegetated cages had a mean growth rate three times higher than cages with gravel and fine mud (Jeffres et al. 2008) (**Fig. 5**). The results have been confirmed for Atlantic cod and white hake (*Urophycis tenuis*) that showed higher growth rates in seagrass compared to sandy areas (Tupper & Boutilier 1995, Renkawitz et al. 2011). Naturally, the prey species available in the two habitats differed but depending on the season the density and number of taxa were very similar in seagrass and sandy areas. The presence of structures has further positive effects on the energy demands of juvenile fish as it lowers the metabolic rate (Millidine et al. 2006). When animals move into areas without shelter they need to be vigilante and prepared to escape predators or competitors. Atlantic salmon (*Salmo salar*) therefore had a 30% higher oxygen consumption in areas without shelter compared to areas with ledges providing shelter (Millidine et al. 2006).

Figure 5. Growth rates of Chinook salmon (*Oncorhynchus tshawytscha*) reared in cages with or without vegetation. From Jeffres et al. 2008

The food items in cod stomachs in **Paper II** changed from small species (Gammaridae) prior to restoration to prey of a higher food quality species such as Galatheidae, Brachyura and fish (although the latter was only borderline significant). The increase in biomass and abundance of prey in cod stomachs demonstrates an increase in fitness caused by the habitat improvement i.e. the boulder reef restoration. Although growth rates was not compared before and after restoration, the increased energy content of prey after restoration is expected to have increased growth rates of cod. In addition, the cod would require less time searching and pursuing prey and thus reducing energy costs, which would further increase growth rates.

Effect on animal body-size

Studies on substrate selection in flatfish show a strong positive relationship between burying ability and sediment choice where small juveniles preferred fine sand and larger juveniles preferred coarse sand (Tanda 1990, Gibson & Robb 2000, Stoner & Ottmar 2003). The same pattern exists for Atlantic cod where young juveniles prefer a finer substrate such as gravel or low bathymetric relief compared to older juveniles that prefer rocks and boulders and high bathymetric relief (Gregory & Anderson 1997). These studies all concur that the sediment preference has to do with defense and shelter from predators. Furthermore, studies have suggested that animals perceive and use habitat architecture based on their own body size and that there exists a relationship between animal body-size and benthic habitat structures (Morse et al. 1985, reviewed by Schmid 2000, Robson et al. 2005). The addition of structural complexity to a benthic environment would thus be expected to result in a higher proportion of larger individuals. As hypothesised, the increased structural complexity of the restored boulder reef increased the proportion of larger individuals overall and specifically for species such as Atlantic cod and ballan wrasse (*Labrus bergylta*) (**Paper II**). In addition, adult saithe that was an infrequent visitor on the reef became more abundant after restoration. Additional studies on the restored reef revealed that harbour porpoise (*Phocoena phocoena*) was observed more frequent on the reef and stayed for longer periods compared to before restoration of the structures (Mikkelsen et al. 2013). The observed effect of reef restoration on the abundance of larger individuals should both be seen as an effect of the increased complexity of the reef and thus increase in shelter from predators, but also of the increased food availability demonstrated in **Paper III**.

Conclusion on the effect of habitat structure on growth and animal body-size

This thesis showed that an increase in structural complexity affected the size distribution of some species (**Paper II, III**). Furthermore, the size of the added structures affected the size of the organisms associated with it. The established biogenic reef exhibited an increase in abundance of smaller fish (gobies) (**Paper I**), whereas the restored boulder reef caused an increase in the mean length of cod and ballan wrasse as well as a general increase in the proportion of smaller and larger fish (**Paper II**) and invertebrates (**Paper III**). The present thesis thus support the connection between habitat structures and body-size of the organisms associated with the structures.

Effect of habitat structure on predator-prey interactions

Effect on survival

Predator foraging success is negatively correlated with habitat complexity (Stoner 1979, 1982, Coull & Wells 1983, Mattila 1992) (**Fig. 6**). An increase in structural complexity can reduce the prey encounter rates and swimming velocities in addition to increase the handling time for fish that depend on visuals to chase and attack their prey (Heck & Orth 1980, Anderson 1984, Gotceitas & Colgan 1989, Horinouchi et al. 2009). The obstacles and shelter provided by the benthic structures therefore also increase the survival rate of prey species (e.g. Dean & Connell 1987, Tupper & Boutilier 1995, 1997, Stoner 2009) (**Fig. 6**). Juveniles of several marine fishes such as Atlantic cod show a preference for areas of high structural complexity, e.g. vegetated or hard bottom areas, which provide shelter from predation (Pihl & Wennhage 2002, Lindholm & Auster 2003, Lindholm et al. 2007). As they grow older, they are less dependent on specific habitat types, probably as a consequence of a lower vulnerability to predation as speculated by Seitz et al. (2014). In the absence of predators, fish often show preferences for the habitat that offers the easiest prey or the highest growth rates (Tupper & Boutilier 1995, Gotceitas et al. 1995, Persson et al. 2012). This supports the ideal free distribution theory proposed by Fretwell (1972), where mobile organisms will forage in those habitats that deliver the highest energetic return. However, it is not always the preferred habitat that provides the lowest mortality risk and there is a trade-off between energy gain and fast growth into size refuge from predators on one side and immediate predation risk on the other. Several studies have demonstrated that when introduced to an active predator, the prey seeks shelter in areas of high complexity such as vegetation (Mattila 1992, Gotceitas et al. 1995, Jordan et

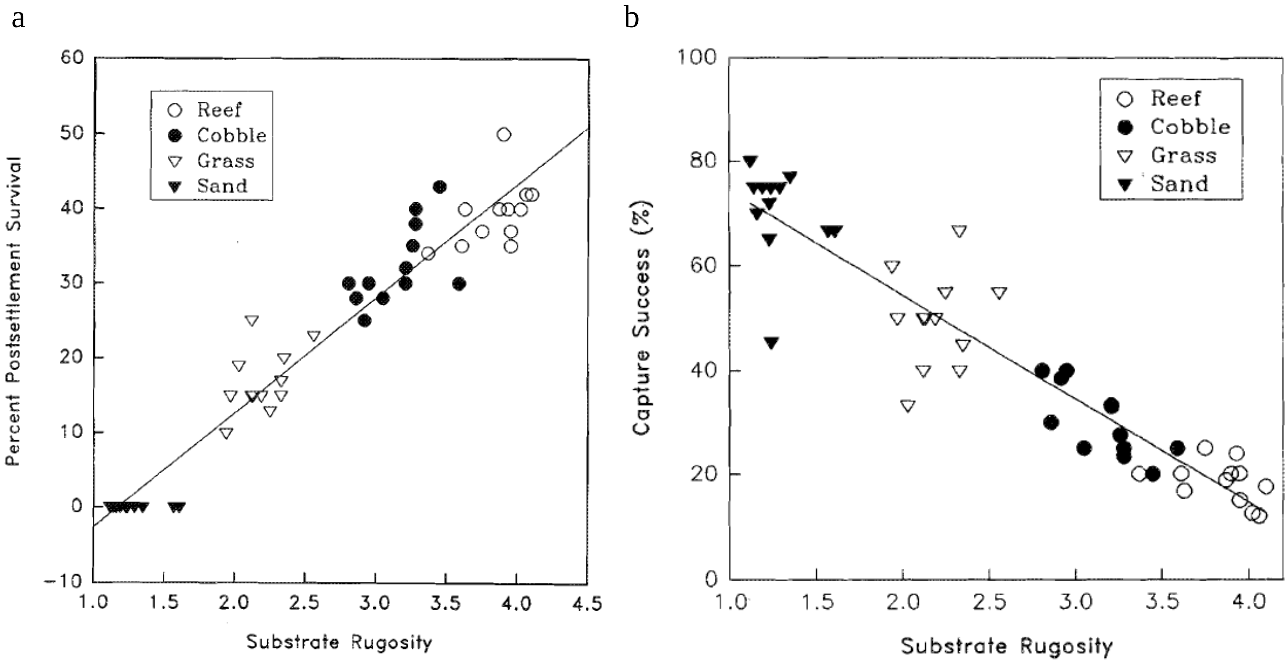

Figure 6. The effect of substrate rugosity on (a) post settlement survival of 0-group cod (*Gadus morhua*) and (b) capture success of predators on 0-group cod. From Tupper & Boutilier 1995.

al. 1996) or hard bottom areas (Gotceitas et al. 1995, Ross et al. 2007). It is thus speculated that, in nature where predators always lurk, vegetated areas are the most profitable as the juvenile cod can,to some degree, continue foraging and are less disturbed by the presence of a predator (Persson et al. 2012).

Conclusion on the effect of habitat structure on predator-prey

The increase in abundance and biodiversity observed in **Paper I, II, III** and the increase in residence time for cod in **Paper IV** suggest increased survival on the established or restored structures. This is likely due to increase in shelter availability from predators provided by the increased structural complexity. In **Paper IV**, only 53% of the released, tagged cod were registered in the study area before restoration while 94% were registered afterward. Further, merely one cod was observed in the study area at 12 weeks prior to restoration while most cod were still present in the study area at 12 week after restoration. It can only be speculated why the cod disappeared so quickly from the study area before the boulder reef was restored, although statistically, the mean length of fish that were registered in the study area was significantly higher than those that did not. One possible explanation could be predation, as the study area prior to restoration offered limited structural complexity and therefore, perhaps lacked shelter from predation. However, further studies are needed to clarify if restored habitats increase the survival of the present species, as no studies have, to the author’s knowledge, addressed this question directly.

EVALUATION OF THE METHODOLOGY

This chapter evaluates the methodology utilized for establishment or restoration of habitat structures. Relevant literature covering aspects of best practices and future perspectives is included.

Biogenic reef (Paper I)

The establishment of biogenic reefs

Bivalves are ecosystem engineers as they modify the benthic environment and influence the health of other organisms (Jones et al. 1994). Biogenic reefs have been recognized as essential habitats for fish and several economically important macroinvertebrates (Jones & Clare 1977, Coen et al. 1999, Seitz et al. 2014). Additionally, it has been shown that biogenic reefs offer ecosystem services such as reducing turbidity and improving water quality through suspension feeding (Riemann et al. 1988, Coen et al. 2007, Nielsen & Maar 2007), thereby facilitating greater light penetration and hence growth of beneficial seagrasses (Newell & Koch 2004). The benefits of biogenic reefs are thus plentiful but a number of species are threatened to near commercial extinction (Wolff 2000, Lotze 2005). This makes bivalves ideal structuring organisms for consideration in habitat restoration projects. This is reflected in the increasing number of biogenic reef restoration activities utilizing bivalves, a notable example being the American oyster (*Crassostrea virginica*) and the restoration attempts in the United States (Brumbaugh et al. 2007).

The study site of **Paper I** was previously dominated by blue mussel beds (Rask et al. 2000). However, eutrophication and hypoxia events were believed to have degraded the benthic habitats with an associated decline in fish populations. The local recreational fisheries organization was very active and their concern for their local environment initiated the establishment of blue mussel beds. The historical position of mussel beds was not recorded for use in this study, making it a restoration of the general function of the biogenic reef rather than of a specific reef site. Given the enclosed nature of the embayment it was deemed that reef function and ecosystem services were of a higher importance than the precise position of the reef.

The method of establishing a biogenic reef

The production of blue mussels on suspended long lines/on hemp sacks was a more ecologically sustainable method compared to transplanting blue mussels by destructive dredging. We were also able to test two new methods and evaluate which was the most effective both in time and labour. Other bivalve restoration projects (e.g. when dealing with endangered species) have collected the focus species in similar non-destructive ways such as collection by rake or hand (McDermott et al. 2008, Fariñas-Franco & Roberts 2014). The collection of seeds is a major task where crowdsourcing (“outsourcing” to a “crowd”) and the use of local volunteers can be applied with great advantages (McDermott et al. 2008). Volunteers contributed to **Paper I** with the harvest and deployment of live blue mussels and mussel shells. Crowdsourcing allowed us to conduct the experiments cost-effectively although it did cause challenges in the planning and implementation processes. The involvement of volunteers can be recommended in future ecological improvement and restoration projects, and the stakeholders themselves suggested that this close collaboration with the local community should be best practice in all future restoration projects. As long as the projects evolve with researchers and local managers, this development of bottom-up initiated projects may be beneficial to society and increase environmental awareness of the local community (Grese et al. 2000). The volunteers' motivation for contributing to restoration projects etc. is often the benefits for future generations and that they develop a "friendship" with nature and a sense of community with other volunteers in the process (Schroeder 2000). Citizen science (the participation of volunteers in scientific investigations) is increasingly contributing to environmental research (Huddart et al. 2016). The same development is seen in Denmark in recent projects where citizens monitor the biodiversity on land and in the coastal areas through mobile applications ("Det Store Naturtjek" by The Danish Society for Nature Conservation and "Opdag Havet" by World Wildlife Foundation). It is thus to be expected that crowdsourcing and citizen sciences will occur more frequently in the future and given the right planning, this could be more cost-efficient than the traditional scientific methods of data collection and sampling.

The monitoring of the established biogenic reef

On a local scale we succeeded in increasing the abundance and diversity of fish through the establishment of blue mussel beds (**Paper I**). On the mussel structures, a threefold higher abundance of small fish was observed, compared to adjacent sandy bottoms. This was investigated through video recordings of the sea floor. The effect was, however, difficult to demonstrate on a larger scale using gill nets. The importance of sampling gear that matches the scale of the structures is thus evident.

We were unable to demonstrate an effect of the established mussel beds on water quality (**Paper I**). However, other studies concur that the effect on water quality can be difficult to quantify in large water bodies (Grabowski & Peterson 2007). Based on the findings of Petersen et al. (2013), we calculated that an increase in secchi depth of 1.5 m in the study area would have required at least 13 times larger mussel production than the 28 tons deployed prior to secchi depth sampling in this thesis.

The established mussel beds in (**Paper I**) experienced very high predation rates from an unusually large starfish population. The abundances of starfish increased up to 32-fold in the study area in 2011. High abundances of starfish were also reported from adjacent waters (Lille Belt) (personal comment, Allan Buch, president of the Danish Fishermen's Association). As mussels increase their survival through aggregation (Okamura 1986) it is possible that larger patch sizes of the established mussel beds could have increased bivalve survival in **Paper I**. However, the structures comprised by the empty mussel shells are just as important as live mussels as they still function as shelter for associated fauna (Palomo et al. 2007, Norling & Kautsky 2007). The threefold increase in the abundance of small fish in the present study support the findings that the function of the shell structures as fish habitat remained intact despite the loss of live blue mussels.

Conclusion on evaluation of the methodology of biogenic reef establishment

It was possible to establish blue mussel beds cost-effectively through crowdsourcing and suspended long-lines. This method can be applied to many other geographic locations where mussel spat are abundant. The mussel bed structures increased biodiversity and a higher abundance of small fish. It can thus be concluded that the established blue mussel beds improved the benthic habitats for fish on a local scale in the study area probably by providing increased prey availability and shelter from predators.

Boulder reef (Paper II, III, IV)

The establishment of boulder reefs

Hard bottom habitats and the associated vegetation are highly productive and provide shelter for myriads of prey organisms such as amphipods and gastropods (Christie et al. 2009). Boulder reefs thus provide good feeding opportunities for many marine species. To the author's knowledge at the time of publication, no boulder reef has previously been restored, however, artificial hard bottom habitats have been established to increase fish abundance e.g. for fishery (Thrush & Dayton 2002, Dupont 2008). Furthermore, studies have shown that the boulder types used in the construction of reefs, may determine whether the boulders will be colonized by algae (sandstone) or barnacles (synthetic basalt) (Green et al. 2012).

The extraction of boulders for the construction industry had left the study area Læsø Trindel a degraded and unstable habitat. As Læsø Trindel is a NATURA 2000 area it was thus restored according to the EU legislation (The Danish Nature Agency 2013). This restoration took place prior to the commencement of this PhD (Stenberg et al. 2015), and this thesis will thus not evaluate the actual restoration method.

The monitoring of the restored boulder reef

This thesis showed that it was possible to evaluate habitat quality based on detailed observations of cod residence time (**Paper IV**). Based on the theory and studies by Lindell (2008) and Layman et al. (2014), the increased residence time for cod, in the present thesis, indicated an increase in cod fitness and habitat improvements caused by the restoration. The stomach content of cod also increased both in biomass and abundance of prey (**Paper III**), which also illustrates habitat improvements through increased prey availability. This thesis is thus a unique opportunity to validate the use of fish behaviour in evaluation of restoration success. Restoration projects are usually evaluated based on species presence and richness or enhancement in abundance (Ruiz-Jaen & Aide 2005, **Paper II**), but detailed observations of animal behaviour of a few key species can be a more cost-effective method than investigating the presence/absence of all species (Lindell 2008).

Conclusion on the evaluation of methodology of boulder reef restoration

Previous studies of the restored boulder reef at Læsø Trindel showed a positive effect on the presence of harbour porpoise (Mikkelsen et al. 2013). The papers of this thesis (**Paper II, III, IV**) concur and conclude that the boulder reef restoration was a success as we demonstrated a positive effect on benthos and fish. This thesis show unique results from the first ever restored boulder reef and the results are thus highly relevant for future management of degraded hard bottom habitats.

Perspectives for establishment or restoration of habitat structures

When planning a restoration project, it is of paramount importance that a thorough investigation of the historical as well as the present habitat is carried out. When restoring boulder reefs or other inorganic structures, the deployed boulders or reef material may sink into an unsupportive seabed or become buried due to sediment transport (Länsstyrelsen 2007, The Danish Nature Agency 2013). Equally, with bivalve restoration projects, selecting areas that do not receive a natural supply of mussel spat, from their own or other reefs' spawning, will result in the reef not sustaining itself past the current generation (Carbines et al. 2004, Geraldi et al. 2009). In either case, the implemented habitat improvements prove redundant in the long term. In the worst case scenario the structures are potentially a sink for oxygen consumption and has negative impact on the surrounding environment (Møhlenberg et al. 2008). To avoid this oxygen sink, one should take advantage of the lessons learned by others and follow the guidelines developed for e.g. mussel bed production (Brumbaugh et al. 2006) or boulder reef restoration (The Danish Nature Agency 2013). These guidelines, as well as other studies on restoration success (Baine 2001, van Diggelen et al. 2001) state the importance of deciding on achievable and measurable goals and the involvement of the local community. Furthermore, proper monitoring is crucial if we are to evaluate whether the project was a success or not and perhaps compare results between studies (Rogers & Allen 2012). On this note, and with the increasing number of locally induced habitat restoration or improvement projects, it is important to maintain the close cooperation with scientists to collect knowledge and further develop the methodology of habitat restoration/improvement. However, due to limited funding and pressure from the public to allocate as much of the resources as possible toward the actual restoration activities, few studies are able to continue to monitor the effect of the restoration/improvements for more than a few years (Brumbaugh et al. 2007). As the full potential of the restoration/improvement may not be achieved for five to seven years (Christie et al. 1998), the abundance and biomass estimates at project termination may under-represent the final outcomes. The need for more long-term studies, perhaps in combination with citizen science and the use of volunteers, should be considered by managers.

Behavioural studies have shown the need for suitable substrate and structures for juvenile fish to hide from predators (Gotceitas & Brown 1993). This suggests that the availability of such substrates could be an important factor affecting subsequent survival of 0+ cod as they settle out of the water column following their pelagic stage and become demersal. It is thus concerning that the extraction of gravel and stones up to 30 cm is still permitted in Danish waters, when populations such as the Kattegat cod are severely depleted (Cardinale & Svedäng 2004). Future studies should investigate the importance of these gravel habitats for economically and ecologically important marine species.

CONCLUSIONS

The present thesis examined the importance of habitat structure for the biodiversity, abundance, size range and behaviour of fish. In this chapter, the results are briefly summarized and conclusions are drawn based on the main findings of this thesis.

Biogenic reef (Paper I)

It was possible to establish blue mussel beds cost-effectively using crowdsourcing and the help from local, volunteer fishermen (**Paper I**). The most effective method both in time and labour proved to be mussel production on hemp sacks followed by direct establishment of the mussel beds. A total of 44 tons of blue mussels were produced and established in beds over an area of 121,000 m^2. This method can be applied to many other geographic locations where mussel spat are abundant. The mussel bed structures improved fish habitat on a local scale resulting in an increased biodiversity and a three times higher abundance of small fish on the introduced mussel structures. In particular, small gobies were observed circling around the structures for extended periods but also larger fish such as cod, trout and flatfish were observed near the established mussel beds. It can thus be concluded that the established blue mussel beds improved the benthic habitats for fish on a local scale in the study area by providing increased prey availability and shelter from predators.

Boulder reef (Paper II, III, IV)

A boulder reef was successfully restored with the addition of 100,000 tons Norwegian quarry boulders deployed on approximately 27,400 m^2 of seabed at Læsø Trindel. The boulders were deposited at three predefined areas thereby stabilizing the existing reef and reintroducing the cave forming reef structures and the shallower parts of the reef.

The restored boulder reef increased the Shannon's diversity index and equitability index for fish species caught in the study area (**Paper II**). The restoration thus increased the biodiversity and resulted in a more even distribution of fish species compared to before restoration, where the study area was dominated by a few wrasse species. This suggests a higher variety of refuge and suitable micro-habitat types after the restoration than before.

The abundance of commercially important species, such as cod and saithe, increased by a factor of between three and six after the boulder reef restoration (**Paper II**). The increase in fish abundance is linked to the availability of benthos, which increased fivefold in abundance and 14-fold in biomass after restoration (**Paper III**). The increased prey availability was most evident for species associated with hard bottom and vegetation habitats reflecting the improved habitat quality attained from the stabilization of the reef, the restored caves and the increased perennial macroalgae species observed in other studies on the reef.

The proportion of larger fish increased after the boulder reef restoration (**Paper II**). The increase in length was especially pronounced for cod and ballan wrasse. This suggests that the restored boulder reef provided better feeding and shelter opportunities for lager fish than before restoration, and also compared to the commercial trawl landings of cod in the surrounding areas. The results, obtained in **Paper IV** based on cod behaviour, showed that prior to restoration the study area was not a suitable habitat for smaller cod. The mean length of fish that were registered in the study area was significantly higher than those that did not. These findings reflect the limited prey availability or lack of shelter from predators prior to restoration and highlight the importance of reef habitats for fish communities and the need for their protection.

A larger fraction of the tagged cod remained in the study area after restoration compared to before (**Paper IV**). The fraction of cod that remained on the reef >50% of the study period, and thus demonstrating high site fidelity, increased sixfold from after restoration. Moreover, cod spent significantly more time in the study area after the restoration. The increased residence time suggests habitat improvements including prey and shelter availability that increase fitness of the tagged cod. The increase in cod fitness was supported by results in **Paper III**, where the prey in cod stomachs increased threefold in terms of biomass and sixfold in terms of abundance post restoration. These results conclude that the residence time of cod is a suitable behavioural trait to evaluate habitat quality and thus restoration success of the boulder reef.

Establishment or restoration of habitat structures

This PhD delivers novel information about the establishment or restoration of benthic habitat structures which is important for future management of degraded coastal habitats. The project investigated the effects of coastal habitat’s structural characteristics on the distribution of fish, whilst maintaining a particular focus on the effect of habitat restoration. The results summarized here show that it was possible to increase the diversity of fish species, increase the abundance of fish (and benthos), increase the size range of fish, and to change the behaviour of cod through the establishment or restoration of complex physical structures in temperate benthic environments. This is, to the author’s knowledge at the time of publication, the first attempt to establish a biogenic reef in Denmark through crowdsourcing in a cost-effective way. Furthermore, this thesis presents the first detailed results of a boulder reef restoration on local fish assemblages. These unique results show that the function of complex benthic substrates can be established or restored for temperate fish species and provide examples of how to carry out such restoration projects for use as a viable management tool.

REFERENCES

Airoldi L, Balata D, Beck MW (2008) The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. J Exp Mar Bio Ecol 366:8–15

Anderson O (1984) Optimal foraging by largemouth bass in structured environments. Ecology 65:851–861

Baine M (2001) Artificial reefs: a review of their design, application, management and performance. Ocean Coast Manag 44:241–259

Bergström U, Bergström L, Carlén I, Isæus M (2011) GIS-baserade metoder för att kartlägga fiskars livsmiljöer i grunda havsområden GIS-baserade metoder i grunda havsområden. Rapport 6427. Stockholm

Bergström L, Sundqvist F, Bergström U (2013) Effects of an offshore wind farm on temporal and spatial patterns in the demersal fish community. Mar Ecol Prog Ser 485:199–210

Blegvad H (1916) Om fiskenes føde i de danske farvande inden for Skagen. Beret til Landbrugsministeriet fra Den danske Biol Stn XXIV:17–72

Bock GM, Thiermann F, Rumohr H, Karez R (2004) Ausmaß der Steinfischerei an der schleswig-holsteinischen Ostseeküste. Jahresbericht Landesamt für Natur und Umwelt des Landes Schleswig-Holstein 2003 8:111–116

Bradshaw AD (1997) What do we mean by restoration? In: Urbanska KM, Webb NR, Edwards P. (eds) Restoration ecology and sustainable development, 1st edn. Cambridge University Press, p 9–14

Bradshaw AD, Chadwick MJ (1980) The restoration of land. Blackwell Scientific Publications, Oxford, United Kingdom

Brumbaugh RD, Beck MW, Coen LD, Craig L, Hicks P (2006) A practitioners guide to the design & monitoring of shellfish restoration projects: An ecosystems services approach. Arlington, NA

Brumbaugh RD, Beck MW, Coen LD, Grizzle RE (2007) A practitioner's perspective on shellfish restoration: why don't we manage shellfish as the ecosystem engineers that they really are? :21–27

Bryant D, Rodenburg E, Cox T, Nielsen D (1995) Coastlines at risk: an index of potential development-related threats to coastal ecosystems. WRI Indic Br (World Resour Institute, Washington, DC)

Burke L, Kura Y, Kassem K, Revenga C, Spalding M, McAllister D (2001) Pilot Analysis of Global Ecosystems. Coastal Ecosystems, Online. Av. WRI, Washington DC

Carbines G, Jiang W, Beentjes MP (2004) The impact of oyster dredging on the growth of blue cod, *Parapercis colias*, in Foveaux Strait, New Zealand. Aquat Conserv Mar Freshw Ecosyst 14:491–504

Cardinale M, Svedäng H (2004) Modelling recruitment and abundance of Atlantic cod, *Gadus morhua*, in the eastern Skagerrak-Kattegat (North Sea): Evidence of severe depletion due to a prolonged period of high fishing pressure. Fish Res 69:263–282

Christie H, Fredriksen S, Rinde E (1998) Regrowth of kelp and colonization of epiphyte and fauna community after kelp trawling at the coast of Norway. Hydrobiologia 376:49–58

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396:221–233

Coen LD, Brumbaugh RD, Bushek D, Grizzle R, Luckenbach MW, Posey MH, Powers SP, Tolley SG (2007) Ecosystem services related to oyster restoration. Mar Ecol Prog Ser 341:303–307

Coen LD, Luckenbach MW (2000) Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation? Ecol Eng 15:323–343

Coen LD, Luckenbach MW, Breitburg DL (1999) The role of oyster reefs as essential fish habitat: A review of current knowledge and some new perspectives. In: Benaka LR (ed) Fish habitat: Essential fish habitat and rehabilitation. American Fisheries Society Symposium, p 438–454

Coull BC, Wells JBJ (1983) Refuges from Fish Predation: Experiments with Phytal Meiofauna from the New Zealand Rocky Intertidal. Ecology 64:1599–1609

Cranfield HJ, Rowden AA, Smith DJ, Gordon DP, Michael KP (2004) Macrofaunal assemblages of benthic habitat of different complexity and the proposition of a model of biogenic reef habitat regeneration in Foveaux Strait, New Zealand. J Sea Res 52:109–125

Dahl K, Lundsteen S, Andersen OGN, Göke C, Rasmussen MB, Stæhr PA, Grønkjær P, Andersen NG, Møhlenberg F (2016) Habitatkvalitet og fødeproduktion. In: Stenberg C, Kristensen LD (eds) Stenrev som gyde- og opvækstområde for fisk. DTU Aqua-rapport nr. 294-2015. DTU Aqua, Institut for Akvatiske Ressourcer, Charlottenlund, p 89–129. In Danish

Dahl K, Lundsteen S, Helmig SA (2003) Stenrev – havbundens oaser, 1st edn. Danmarks Miljøundersøgelser. Gads Forlag, Copenhagen. In Danish

Dahl K, Lundsteen S, Tendal OS (2005) Mejlgrund og Lillegrund. En undersøgelse af biologisk diversitet på et lavvandet område med stenrev i Samsø Bælt. Faglig rapport fra DMU nr. 529.

Dahl K, Stenberg C, Lundsteen S, Støttrup J, Dolmer P, Secher Tendal O (2009) Ecology of Læsø Trindel – a reef impacted by extraction of boulders. Neri Technical Report no. 757. Aarhus

Dean RL, Connell JH (1987) Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. J Exp Mar Bio Ecol 109:249–273

Diggelen R van, Grootjans AP, Harris J a. (2001) Ecological Restoration: State of the Art or State of the Science? Restor Ecol 9:115–118

Dolmer P, Christensen H, Hansen B, Vismann B (2012) Area-intensive bottom culture of blue mussels *Mytilus edulis* in a micro-tidal estuary. Aquac Environ Interact 3:81–91

Dupont JM (2008) Artificial Reefs as Restoration Tools: A Case Study on the West Florida Shelf. Coast Manag 36:495–507

EEA (1999) Environment in the European Union at the turn of the century. State of Environment Report, 1/1999. Copenhagen

Eklöv P (1997) Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). Can J Fish Aquat Sci 54:1520–1531

Eriksson BK, Johansson G, Snoeijs P (1998) Long-term changes in the sublittoral zonation of brown algae in the southern Bothnian Sea. Eur J Phycol 33:241–249

Fariñas-Franco JM, Roberts D (2014) Early faunal successional patterns in artificial reefs used for restoration of impacted biogenic habitats. Hydrobiologia 727:75–94

Ferreira CEL, Goncalves EA, Coutinho R (2001) Community structure of fishes and habitat complexity on a tropical rocky shore. Environ Biol 61:353–369

Fredshavn J, Søgaard B, Nygaard B, Johansson LS, Wiberg-Larsen P, Dahl K, Sveegaard S, Galatius A, Teilmann J (2014) Bevaringsstatus for naturtyper og arter. Habitatdirektivets artikel 17 rapportering.

Freese L, Auster PJ, Heifetz J, Wing BL (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar Ecol Prog Ser 182:119–126

Fretwell SD (1972) Populations in a Seasonal Environment. Princeton University Press, Princeton, New Jersey

Gage JD, Roberts JM, Hartley JP, Humphery JD (2005) Potential Impacts of Deep-Sea Trawling on the Benthic Ecosystem along the Northern European Continental Margin: A Review. Am Fish Soc Symp 41:503–517

Geraldi N, Powers S, Heck K, Cebrian J (2009) Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks. Mar Ecol Prog Ser 389:171–180

Gibson RN (1994) Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. Netherlands J Sea Res 32:191–206

Gibson R, Robb L (2000) Sediment selection in juvenile plaice and its behavioural basis. J Fish Biol 56:1258–1275

Glibert P, Seitzinger S, Heil C, Burkholder J, Parrow M, Codispoti L, Kelly V (2005) The Role of Eutrophication in the Global Proliferation of Harmful Algal Blooms. Oceanography 18:198–209

Godoy E, Almeida T, Zalmon I (2002) Fish assemblages and environmental variables on an artificial reef north of Rio de Janeiro, Brazil. ICES J Mar Sci 59:S138–S143

Gordon JDM (2002) Deep water demersal fisheries. Joint Nature Conservation Committee (JNCC) Available: http://www.jncc.gov.uk/marine/page-2525 (Feb 2016).

Gotceitas V, Brown J (1993) Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93:31–37

Gotceitas V, Colgan P (1989) Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80:158–166

Gotceitas V, Fraser S, Brown J a. (1995) Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Mar Biol 123:421–430

Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: concepts, theory and applications. Elsevier-Academic Press, Amsterdam, p 281–298

Gray JS, Dayton P, Thrush S, Kaiser MJ (2006) On effects of trawling, benthos and sampling design. Mar Pollut Bull 52:840–843

Green DS, Chapman MG, Blockley DJ (2012) Ecological consequences of the type of rock used in the construction of artificial boulder-fields. Ecol Eng 46:1–10

Gregory RS, Anderson JT (1997) Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Mar Ecol Prog Ser 146:9–20

Grese RE, Kaplan R, Ryan RL, Buxton R (2000) Psychological benefits of volunteering in stewardship programs. In: Gobster PH, Hull B (eds) Restoring nature: perspectives from the social sciences and humanities. Island Press, Wahington D.C., p 265 – 280

Hall SJ, Robertson MR, Basford DJ, Fryer R (1993) Pit-digging by the crab *Cancer pagurus*: a test for long-term, large scale effects on infaunal community structure. J Anim Ecol 62:59–66

Heck KL, Orth RJ (1980) Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and motile macroinvertebrate assemblages. Estuar Perspect:449–464

Henderson PA, Seaby RMH, Somes JR (2011) Community level response to climate change: The long-term study of the fish and crustacean community of the Bristol Channel. J Exp Mar Bio Ecol 400:78–89

Hernández-Ávila I, Tagliafico A, Rago N, Marcano J (2012) Composition of decapod crustacean assemblages in beds of *Pinctada imbricata* and *Arca zebra* (Mollusca: Bivalvia) in Cubagua Island, Venezuela: Effect of bed density. Sci Mar 76:705–712

Horinouchi M, Mizuno N, Jo Y, Fujita M, Sano M, Suzuki Y (2009) Seagrass habitat complexity does not always decrease foraging efficiencies of piscivorous fishes. Mar Ecol Prog Ser 377:43–49

Howard AE, Bennet DB (1979) The substrate preference and burrowing behaviour of juvenile lobsters (*Homarus gammerus* (L.)). J Nat Hist 13:433–438

Huddart JEA, Thompson MSA, Woodward G, Brooks SJ (2016) Citizen science: from detecting

pollution to evaluating ecological restoration. Wiley Interdiscip Rev Water
Jackson A (2007) *Ostrea edulis* Native oyster. In: Tyler-Walters H, Hiscock K (eds) Marine Life Information Network: Biology and Sensitivity Key Information Reviews. Plymouth: Marine Biological Association of the United Kingdom, http://www.marlin.ac.uk/species/detail/1146 (Feb 2016)
Jeffres C a., Opperman JJ, Moyle PB (2008) Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. Environ Biol Fishes 83:449–458
Jensen AAC, Collins KJ, Free EK, Bannister RCA (1994) Lobster (*Homarus gammarus*) Movement on an Artificial Reef: The Potential Use of Artificial Reefs for Stock Enhancement. Crustaceana 67:198–211
Jones D, Clare J (1977) Annual and long-term fluctuations in the abundance of fish species inhabiting an intertidal mussel bed in Morecambe Bay, Lancashire. Zool J Linn Soc 60:117–172
Jones C, Lawton J, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386
Jordan F, Bartolini M, Nelson C, Patterson PE, Soulen HL (1996) Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). J Exp Mar Bio Ecol 208:45–56
Jørgensen BB (1980) Seasonal Oxygen Depletion in the Bottom Waters of a Danish Fjord and Its Effect on the Benthic Community. Oikos 34:68–76
Kaiser M, Clarke K, Hinz H, Austen M, Somerfield P, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. Mar Ecol Prog Ser 311:1–14
Karlsen JD (2011) Hot on the tail of hefty Atlantic cod: an interdisciplinary study on the behaviour at ship wrecks in the North Sea. Aarhus University
Kenchington ELR, Gilkinson KD, MacIsaac KG, Bourbonnais-Boyce C, Kenchington TJ, Smith SJ, Gordon DC (2006) Effects of experimental otter trawling on benthic assemblages on Western Bank, northwest Atlantic Ocean. J Sea Res 56:249–270
Kenchington EL, Kenchington TJ, Henry LA, Fuller S, Gonzalez P (2007) Multi-decadal changes in the megabenthos of the Bay of Fundy: The effects of fishing. J Sea Res 58:220–240
Koivisto M, Westerbom M (2012) Invertebrate communities associated with blue mussel beds in a patchy environment: a landscape ecology approach. Mar Ecol Prog Ser 471:101–110
Kostylev VE, Erlandsson J, Ming MY, Williams G a. (2005) The relative importance of habitat complexity and surface area in assessing biodiversity: Fractal application on rocky shores. Ecol Complex 2:272–286
Krause-Jensen D, Carstensen J, Nielsen SL, Dalsgaard T, Christensen PB, Fossing H, Rasmussen M. (2011) Sea bottom characteristics affect depth limits of eelgrass *Zostera marina*. Mar Ecol Prog Ser 425:91–102
Krause-Jensen D, Markager S, Dalsgaard T (2012) Benthic and Pelagic Primary Production in Different Nutrient Regimes. Estuaries and Coasts 35:527–545
Kristensen LD, Stenberg C, Støttrup JG, Poulsen LK, Christensen HT, Dolmer P, Landes A, Røjbæk M, Thorsen SW, Holmer M, Deurs M van, Grønkjær P (2015) Establishment of blue mussel beds to enhance fish habitats. Appl Ecol Environ Res 13:783–798
Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol Lett 13:1419–1434
Länsstyrelsen (2007) Hummerrevsprojektet Slutrapport 2007. Rapport 2007:40.
Layman CA, Jud ZR, Arrington A, Sabin D (2014) Using Fish Behavior to Assess Habitat Quality of a Restored Oyster Reef. Ecol Restor:140–143
Lindell CA (2008) The Value of Animal Behavior in Evaluations of Restoration Success. Restor Ecol 16:197–203
Lindholm J, Auster P (2003) Site utilization by cod in off-shore gravel habitat. Mar Technol Soc J

37:27–34
Lindholm J, Auster PJ, Knight A (2007) Site fidelity and movement of adult Atlantic cod *Gadus morhua* at deep boulder reefs in the western Gulf of Maine, USA. Mar Ecol Prog Ser 342:239–247
Lintas C, Seed R (1994) Spatial variation in the fauna associated with *Mytilus edulis* on a wave-exposed rocky shore. J Molluscan Stud 60:165–174
Lotze HK (2005) Radical changes in the Wadden Sea fauna and flora over the last 2,000 years. Helgol Mar Res 59:71–83
Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–9
Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. Mar Biol 49:317–323
Mackenzie CL, Lynch SA, Culloty SC, Malham SK (2014) Future oceanic warming and acidification alter immune response and disease status in a commercial shellfish species, *Mytilus edulis* L. PLoS One 9:e99712
Mattila J (1992) The effect of habitat complexity on predation efficiency of perch *Perca fluviatilis* L. and ruffe *Gymnocephalus cernuus* (L.). J Exp Mar Bio Ecol 157:55–67
McCormick SD, Hansen LP, Quinn TP, Saunders RL (1998) Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 55:77–92
McDermott S, Burdick D, Grizzle R, Greene J (2008) Restoring ecological functions and increasing community awareness of an urban tidal pond using blue mussels. Ecol Restor 26:254–262
Mikkelsen L, Mouritsen KN, Dahl K, Teilmann J, Tougaard J (2013) Re-established stony reef attracts harbour porpoises *Phocoena phocoena*. Mar Ecol Prog Ser 481:239–248
Millidine KJ, Armstrong JD, Metcalfe NB (2006) Presence of shelter reduces maintenance metabolism of juvenile salmon. Funct Ecol 20:839–845
Møhlenberg F, Murray C, Krause-Jensen D, Naturstyrelsen S (2008) Faglig rapport: Stenrev i Limfjorden: Fra naturgenopretning til supplerende virkemiddel.
Moriarty C, Dekker W (1997) Management of the European eel. Fish Bull 15:110
Morse DR, Lawton JH, Dodson MM, Williamson MH (1985) Fractal dimension of vegetation and the distribution of arthropod body length. Nature 314:731–733
National Research Council (1992) Restoration of aquatic ecosystems. The National Academies Press, Washington DC
Newell R, Koch E (2004) Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries 27:793–806
Nielsen T, Maar M (2007) Effects of a blue mussel *Mytilus edulis* bed on vertical distribution and composition of the pelagic food web. Mar Ecol Prog Ser 339:185–198
Nielsen PE, Petersen EH (2013) Råstofproduktion i Danmark. Havområdet 2012. Copenhagen
Nielsen SL, Sand-Jensen K, Borum J, Geertz-Hansen O (2002a) Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. Estuaries 25:1025–1032
Nielsen SL, Sand-Jensen K, Borum J, Geertz-Hansen O (2002b) Phytoplankton, nutrients, and transparency in Danish coastal waters. Estuaries 25:930–937
Norderhaug KM, Christie H, Fosså JH, Fredriksen S (2005) Fish–macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. J Mar Biol Assoc UK 85:1279
Norling P, Kautsky N (2007) Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. Mar Ecol Prog Ser 351:163–175

Norling P, Kautsky N (2008) Patches of the mussel *Mytilus sp.* are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. Aquat Biol 19:75–87

O'Connor NE, Crowe TP (2007) Biodiversity among mussels: separating the influence of sizes of mussels from the ages of patches. J Mar Biol Assoc UK 87:551–557

Okamura B (1986) Group Living and the Effects of Spatial Position in Aggregations of *Mytilus edulis*. Oecologia 69:341–347

Palomo M, People J, Chapman M, Underwood A (2007) Separating the effects of physical and biological aspects of mussel beds on their associated assemblages. Mar Ecol Prog Ser 344:131–142

Parker VT, Pickett STA (1997) Restoration as an ecosystem process: implications of the mordern ecological paradigm. In: Urbanska KM, Webb NR, Edwards PJ (eds) Restoration ecology and sustainable development, 1st edn. Cambridge University Press, Cambridge, United Kingdom, p 17–32

Persson A, Ljungberg P, Andersson M, Götzman E, Nilsson PA (2012) Foraging performance of juvenile Atlantic cod *Gadus morhua* and profitability of coastal habitats. Mar Ecol Prog Ser 456:245–253

Petersen JK, Timmermann K, Holmer M, Hasler Be, Cordula G, Marianne Z (2013) Miljømuslinger. Muslinger som supplerende virkemiddel. Notat fra DCE - Nationalt Center for Miljø og Energi.

Peterson C, Grabowski J, Powers S (2003) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar Ecol Prog Ser 264:249–264

Pickering H, Whitmarsh D (1997) Artificial reefs and fisheries exploitation: a review of the "attraction versus production" debate, the influence of design and its significance for policy. Fish Res 31:39–59

Pihl L, Wennhage H (2002) Structure and diversity of fish assemblages on rocky and soft bottom shroes on the Swedish west coast. J Fish Biol 61:148–166

Pihl L, Wennhage H, Nilsson S (1994) Fish assemblage structure in relation to macrophytes and filamentous epiphytes in shallow non-tidal rocky- and soft-bottom habitats. Environ Biol Fishes 39:271–288

Prins TC, Small AC (1994) The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde estuary (The Netherlands). Hydrobiologia 282:413–429

Rajasilta M, Eklund J, Kääriä J, Ranta-Aho K (1989) The deposition and mortality of the eggs of the Baltic herring *Clupea harengus membras* L., on different substrates in the south-west archipelago of Finland. J Fish Biol 34:417–427

Rask N, Bundgaard Madsen H, Larsen S (2000) Vandmiljøovervågning: Kystvande 1999.

Renkawitz MD, Gregory RS, Schneider DC (2011) Habitat dependant growth of three species of bottom settling fish in a coastal fjord. J Exp Mar Bio Ecol 409:79–88

Reubens JT, Rijcke M De, Degraer S, Vincx M (2014) Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore wind farms. J Sea Res 85:214–221

Richardson K, Jørgensen BB (1996) Eutrophication: definition, history and effects. Eutrophication a Coast Mar Ecosyst:1–9

Riemann B, Nielsen T, Horsted S, Bjørnsen P, Pock-Steen J (1988) Regulation of phytoplankton biomass in estuarine enclosures. Mar Ecol Prog Ser 48:205–215

Risk MJ (1972) Fish diversity on a coral reef in the Virgin Islands. Atoll Res Bull:7

Robson BJ, Barmuta LA, Fairweather PG (2005) Methodological and conceptual issues in the search for a relationship between animal body-size distributions and benthic habitat architecture. Mar Freshw Res 56:1–11

Rogers MW, Allen MS (2012) An Ecosystem Model for Exploring Lake Restoration Effects on

Fish Communities and Fisheries in Florida. Restor Ecol 20:612–622

Ross PM, Thrush SF, Montgomery JC, Walker JW, Parsons DM (2007) Habitat complexity and predation risk determine juvenile snapper (*Pagrus auratus*) and goatfish (*Upeneichthys lineatus*) behaviour and distribution. Mar Freshw Res 58:1144

Ruiz-Jaen MC, Aide TM (2005) Restoration success: How is it being measured? Restor Ecol 13:569–577

Schmid PE (2000) Fractal properties of habitat and patch structure in benthic ecosystems. Adv Ecol Res 30:339–401

Schroeder HW (2000) The restoration experience: Volunteers' motives, values, and concepts of nature. In: Gobster PH, Hull RB (eds) Restoring nature: perspectives from the social sciences and humanities. Island Press, Washington DC, p 247–264

Seed R (1996) Patterns of Biodiversity in the Macro-Invertebrate Fauna Associated with Mussel Patches on Rocky Shores. J Mar Biol Assoc United Kingdom 76:203–210

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological Value of Coastal Habitats for Commercially and Ecologically Important Species. ICES J Mar Sci 71:648–665

Sheehy MRJ, Prior AE (2008) Progress on an old question for stock assessment of the edible crab *Cancer pagurus*. Mar Ecol Prog Ser 353:191–202

Stål J, Pihl L, Wennhage H (2007) Food utilisation by coastal fish assemblages in rocky and soft bottoms on the Swedish west coast: Inference for identification of essential fish habitats. Estuar Coast Shelf Sci 71:593–607

Stenberg C, Kristensen LD (Eds) (2015) Stenrev som gyde- og opvækstområde for fish. DTU Aqua-rapport nr. 294-2015. DTU Aqua, Institut for Akvatiske Ressourcer, Charlottenlund. In Danish

Stenberg C, Støttrup J, Dahl K, Lundsteen S, Göke C, Andersen ON (2015) Ecological benefits from restoring a marine cavernous boulder reef in Kattegat, Denmark. DTU Aqua report no. 289-2015. Copenhagen

Stoner AW (1979) Species-specific predation on amphipod crustacea by the pinfish Lagodon rhomboides: Mediation by macrophyte standing crop. Mar Biol 55:201–207

Stoner AW (1982) The influence of benthic macrophytes on the foraging behaviour of pinfish, Lagodun rhombiodes (Linnaeus). J Exp Mar Bio Ecol 58:271–284

Stoner AW (2009) Habitat-mediated survival of newly settled red king crab in the presence of a predatory fish: Role of habitat complexity and heterogeneity. J Exp Mar Bio Ecol 382:54–60

Stoner AW, Ottmar ML (2003) Relationships between size-specific sediment preferences and burial capabilities in juveniles of two Alaska flatfishes. J Exp Mar Bio Ecol 282:85–101

Støttrup JG, Stenberg C, Dahl K, Kristensen LD, Richardson K (2014) Restoration of a Temperate Reef: Effects on the Fish Community. Open J Ecol 4:1045–1059

Suchanek TH (1994) Temperate Coastal Marine Communities: Biodiversity and Threats. Am Zool 34:100–114

Sundblad G, Bergström U, Sandström A, Eklöv P (2014) Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES J Mar Sci 71:672–680

Svane I, Setyobudiandi I (1996) Diversity of associated fauna in beds of the blue mussel *Mytilus edulis* L.: effects of location, patch size, and position within a patch. Ophelia 45:39–53

Tanda M (1990) Studies on burying ability in sand and selection to the grain size for hatchery-reared marbled sole and Japanese flounder. Nippon Suisan Gakkaishi 56:1543–1548

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

The Danish Nature Agency (2013) Best practice for restoration of stone reefs in Denmark (codes of

conduct). LIFE06 NAT/DK000159 - Blue Reef project. Final Technical Report. Annex 9. Copenhagen
The Danish Nature Agency. (2013) Natura 2000-basisanalyse for Læsø Trindel og Tønneberg Banke. Natura 2000-område nr. 192 Habitatområde nr. 168. Copenhagen
Thomasson MA, Tunberg BG (2005) Composition and vertical distribution of the motile epifauna on a vertical rock wall in Gullmarsfjorden, western Sweden, using an alternative sampling approach. Mar Biol Res 1:107–117
Thrush S (1986) Spatial heterogeneity in subtidal gravel generated by the pit-digging activities of *Cancer pagarus*. Mar Ecol Prog Ser 30:221–227
Thrush SF, Dayton PK (2002) Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annu Rev Ecol Syst 33:449–473
Tupper M, Boutilier RC (1995) Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 52:1834–1841
Tupper M, Boutilier RG (1997) Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Mar Ecol Prog Ser 151:225–236
Vogt H, Schramm W (1991) Conspicuous decline of Fucus in Kiel Bay (western Baltic): what are the causes? Mar Ecol Prog Ser 69:189–194
Wahle RA, Steneck RS (1991) Recruitment habitats and nursery grounds of the American lobster *Homarus Americanus*: a demographic Bottleneck? Mar Ecol Prog Ser 69:231–243
Walter U, Liebezeit G (2003) Efficiency of blue mussel (*Mytilus edulis*) spat collectors in highly dynamic tidal environments of the Lower Saxonian cost (southern North Sea). Biomol Eng 20:407–411
Watling L, Norse EA (1998) Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting. Conserv Biol 12:1180–1197
Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes Ar, Kendrick GA, Kenworthy Wj, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc Natl Acad Sci USA 106:12377–12381
Wennhage H, Pihl L (2002) Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. J Fish Biol 61:207–228
Wolff WJ (2000) Causes of Extirpations in the Wadden Sea, an Estuarine Area in The Netherlands. Conserv Biol 14:876–885

Paper I

Establishment of blue mussel beds to enhance fish habitats

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ESTABLISHMENT OF BLUE MUSSEL BEDS TO ENHANCE FISH HABITATS

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Abstract. Human activity has impacted many coastal fjords causing degeneration of the structure and function of the fish habitats. In Nørrefjord, Denmark, local fishermen complained of declining fish catches which could be attributed to eutrophication and extraction of sediments over several decades. This study aimed to establish blue mussel beds (*Mytilus edulis*) to increase structural complexity and increase the abundance of fish and epifauna in Nørrefjord. It was expected that the mussels would improve water transparency and increase the depth range and coverage of eelgrass (*Zostera marina*). New methods for mussel production and -bed construction were investigated in collaboration with local volunteer fishermen. The effect of the artificial mussel beds was most evident on a small scale. Video observations directly at the beds (Impact area) demonstrated increased biodiversity and a three times higher abundance of mesopredator fish compared to the Control area. Water clarity and eelgrass coverage were unchanged. Two methods for establishing mussel beds were tested. A total of 44 tons of blue mussels were produced and established in beds over an area of 121,000 m^2. Production of blue mussels directly on hemp sacs hanging on long-lines was the most effective method. This new method is potentially a useful management tool to improve fish habitats.
Keywords: *habitat complexity, biogenic reef, fish community, benthos, volunteer.*

Introduction

Coastal habitats are under great anthropogenic pressure and 85% of the European coastlines are estimated to be degraded (Bryant et al., 1995; EEA, 1999). Eutrophication, overfishing and destructive dredging fishery have severely affected shellfish and biogenic reefs (Airoldi and Beck, 2007). These pressures may also affect the population structure of fish (Sundblad et al., 2014) as the coastal habitats are important for many commercial fishes for spawning, feeding and as nursery area (Seitz et al., 2014).

Habitat complexity in coastal habitats is an important component for a number of fish species as more complex bottom structures provide more shelter opportunity from predators and a higher abundance of prey than bare bottom sediments (Heck and Wetstone, 1977; Luckhurst and Luckhurst, 1978; Nelson and Bonsdorff, 1990). The abundance and biodiversity of fauna living within a biogenic reef of bivalves, increase with complexity and structure area, and promotes fish growth and diversity (Carbines et al., 2004; Norling and Kautsky, 2007; 2008). Especially smaller fish species such as common goby (*Pomatoschistus microps*), rock goby (*Gobius paganellus*) and butterfish (*Pholis gunnellus*) but also larger fish like flatfishes use mussel beds as habitat for either direct foraging, breeding or as nursery area (Jones and Clare, 1977). Predatory fish are attracted to the structures by the abundance of prey. The overall effects of increased complexity can thus be relatively substantial for fish. Apart from improving coastal habitats by increasing the complexity (McDermott et al., 2008), mussels are filter feeders and remove suspended inorganics, phytoplankton and detrital particles. The filtration process reduces turbidity and generally improves water quality (Riemann et al., 1988; Nielsen and Maar, 2007). The improved water transparency leads to better conditions for benthic primary producers e.g. sea grasses (Newell and Koch, 2004), allowing them to spread into deeper areas.

Nørrefjord, Denmark, is representative for many coastal areas in northern Europe. It has been subject to substantial nitrogen loadings from agriculture during the last three to four decades (Rask et al., 2000). High nitrogen loadings are known to reduce water transparency and increase the extent and frequency of oxygen depletion events (Krause-Jensen et al., 2011; 2012; Wulff et al., 2014). However, in the last decade, nitrogen loading has dropped markedly in Nørrefjord, whereas phosphorous has remained unchanged but at a low level (data, The Danish Natural Environment Portal, miljoeportal.dk) due to intensive improvements in sewage treatment during the 1980s (Ærtebjerg et al., 2003). Further, the fjord has experienced extraction of sand and gravel from 1950-1990 (N.C. Christensen, local fisherman, pers. com.). Extraction of resources from shallow coastal areas reduces the complexity of the bottom and the habitat quality (Nielsen and Petersen, 2013). In other coastal areas in Denmark, dredging activities with towed fishing gears for fin- and shellfish (Dolmer and Frandsen, 2002; Kaiser et al., 2006) also deteriorate habitat quality. Furthermore, climate change, increased water temperature and acidification may impact coastal habitats (IPCC, 2014; Mackenzie et al., 2014). All these pressures have resulted in deteriorated habitats and a decline in bottom fauna and fish biomass (Pihl et al., 2005; Holm, 2005; Christiansen et al., 2006). Nørrefjord was previously dominated by blue mussel beds (Rask et al., 2000) but hypoxia events is believed to have degraded the benthic habitats with an associated decline in fish populations. This general deterioration of the fjord is of great concern to the local recreational fishermen, who experience declining fish catches. The recreational fishermen therefore initiated this project to improve conditions for fish by promoting fish habitats in Nørrefjord. This project is unique through the close collaboration between local stakeholders, local managers and researchers.

Bivalve restoration is known to have a positive effect on fish communities (reviewed by Peterson et al., 2003). Most studies focus on oyster beds, but the function of structure is more important than the species comprising the structure (Palomo et al., 2007; Norling and Kautsky, 2007). Therefore it was hypothesized that establishment of mussel beds could, in a manner similar to oyster beds, improve fish habitats. When establishing cultured mussels, it is standard procedure to dredge natural bottom mussels for seeds

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and then transplant the mussels to a different area from a specialized vessel (Dolmer et al., 2012). Neither the destructive dredging nor the expensive machinery was an option in this project in Nørrefjord.

The primary aim of this study was to test if establishment of blue mussel beds would have a positive effect on abundance of fish and epifauna. It was also hypothesized that the established mussel beds would improve water transparency followed by increase in eelgrass (*Zostera marina*) depth range and coverage. The secondary aim was to develop an efficient and effective method for production of suspended blue mussels for the establishment of bottom mussel beds in a Danish fjord using voluntary labour, as this had not been attempted before.

Materials and Methods

Study area

The field study was conducted during 2010 and 2011 in Nørrefjord, Helnæs Bight (10 7.17E 55 9.10N) south-west of the Island of Funen, Denmark (*Fig. 1*). The fjord is a protected bay with two connections to the strait Lille Belt between Funen and the Jutland Peninsula. The mean water depth is 5.5 m and the maximum depth is 12 m (Rask et al., 2000). Two sites resembling each other in terms of depth, sediment and eelgrass cover were chosen 1 km apart, one was the Control and one was the Impact area (*Fig. 1*).

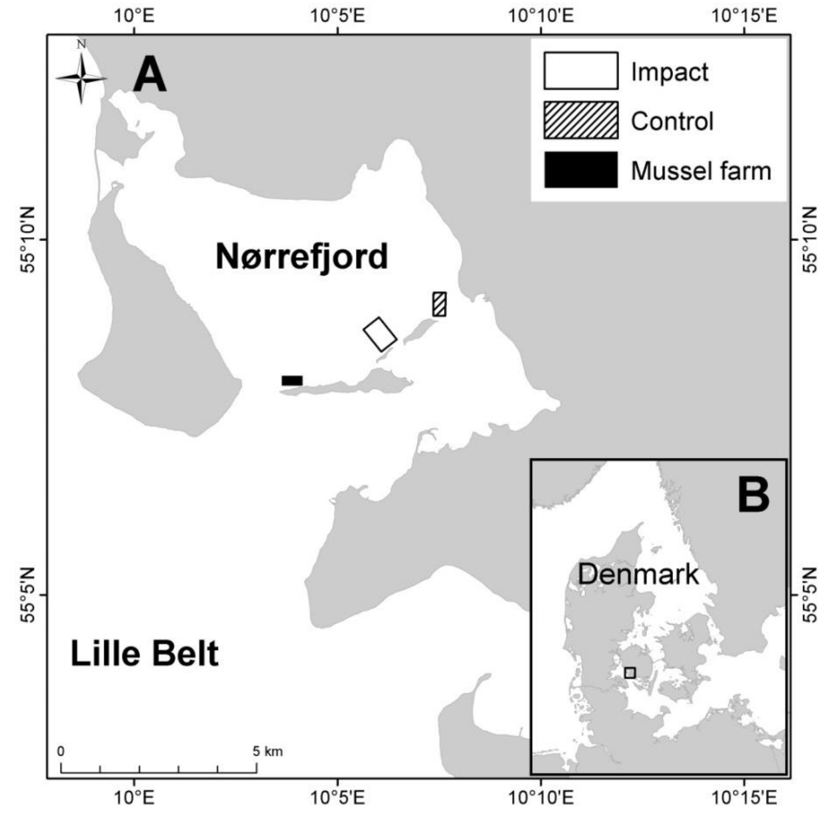

Figure 1. *Study area. A) Location of the mussel farm, the Impact area, and the Control area. B) Location of Nørrefjord in Denmark.*

Establishment of blue mussel beds

A mussel collection site (mussel farm) was established with help from a local consultant (Nordshell A/S) (*Fig. 1*). The mussel farm consisted of long-line systems (7 x 200 m length) maintained floating by gradually increasing the number of buoys as the weight of the produced mussels increased over the summer.

Blue mussel beds were established on the fjord bottom at 4-6 m depth within the Impact area (*Fig. 2a*). The mussel beds where constructed to increase the complexity of the bottom substrate to improve the beds' value as fish habitat. The overall bed structure was constructed in a patchy distribution to imitate natural mussel beds. The mussel beds were constructed as piles of 1 m diameter and 0.5 m height (= one mussel bed). This was done by piling 28 kg of mussels on top of degradable hemp sacks through a tube (40 cm diameter, 6 m length). Half the piles were placed on top of 3 hemp sacks (60-100 L) containing mussel shells (40 L per sac), thus producing 3-dimensional structures on the seafloor. Another 25% of the piles consisted of mussels placed directly on the fjord bottom without hemp sacks. The remaining 25% consisted of hemp sacks with mussel shells. All mussel beds were placed in grids with 3-10 m distance between single beds resulting in a mussel density of 2.8-9.3 kg mussel m^{-2}.

Effect analysis

Before commencing the effect analysis, diver and video observations were made to estimate the survival rate of the blue mussels and to confirm that the structures still remained on the fjord bottom. No systematic analysis was made based on diver and video observations. However, a rough estimate of the mussel survival rate was found based on the observations.

The effect of the constructed mussel beds was measured in a BACI design, including investigations *before* mussel bed establishment (summer of 2010) and one year *after* mussel bed establishment (summer of 2011). All analysis took place in both *control* and *impact* area. The effect analysis sought to clarify the effect of the mussel beds on fishes, epibenthic invertebrates and important environmental parameters presented in the following sections.

Eelgrass and water quality

Eelgrass coverage in the Impact area and Control area was mapped 1) to locate areas suitable for mussel bed establishment and 2) to analyse the effect of the mussel beds on eelgrass coverage *before* and *after* mussel bed establishment (*Table 1, Fig. 2*). Eelgrass coverage was mapped by *in situ* video monitoring of the fjord bottom from a slow drifting boat. GPS position of the drop camera (600 TV lines) and the associated eelgrass coverage was logged every 2 min. Eelgrass coverage was analysed in 5 categories: 0 = no eelgrass, 1 = dead shoots, 2 = single plants, 3 = thin coverage or patches, 4 = dense beds of eelgrass. These categories corresponded to a percentage cover of 0 = 0%, 1 = 0 % (dead shoots), 2 = 1-25%, 3 = 26-75%, 4 = 75-100%. Mussel beds were placed in areas within the Impact area where there was, generally, no eelgrass to avoid damaging eelgrass beds.

The effect of the mussel beds on water transparency was investigated by measuring secchi depth, and measurements were carried out weekly from May to September *before* and *after* mussel bed establishment.

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Epibenthic samples

Benthic invertebrates were quantified in the Control area and Impact area *before* and *after* mussel bed establishment using an epibenthic sledge (Modified Ockelman Sledge, KC Denmark, Denmark) (*Table 1*). The sledge was dragged 30 sec at 1 kn over the seafloor at 4-6 randomly selected stations in the two areas, in the depth range of mussel bed establishment (4-6 m), to sample invertebrates and other smaller organisms living on the surface of the bottom substrate. The density of all fauna was estimated based on the area covered by the sledge on each tow (4.6 m^2). All organisms were counted and determined to lowest possible taxonomical group. Fish, blue mussels and snails were not included in this analysis as they could not be quantified properly from sampling with the epibenthic sledge.

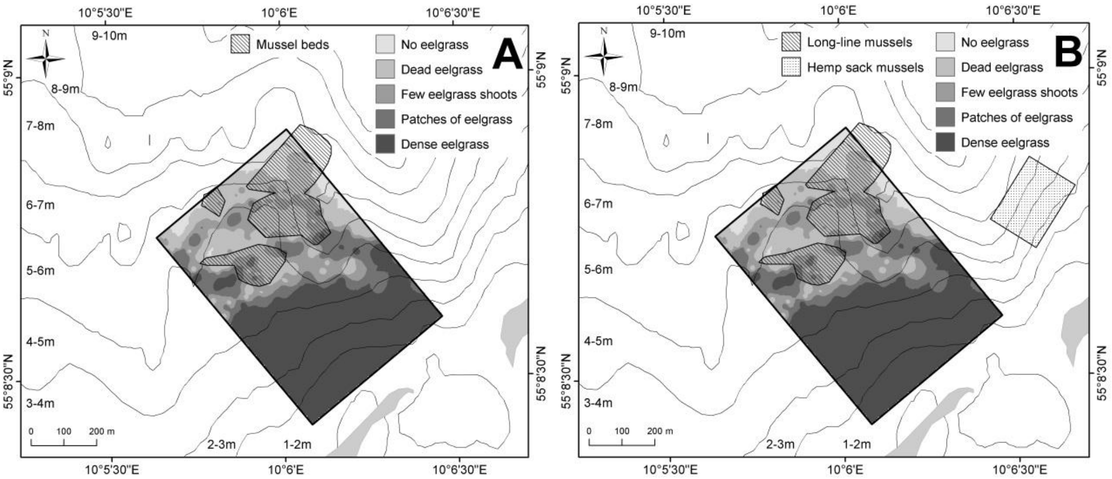

Figure 2. *A) Mussel beds were established in Impact area. B) Two different methods of blue mussel production and establishment of mussel beds were tested in 2010 and 2011, respectively. Eelgrass cover is based on data from 2010.*

Fish community

Fish distribution and abundance was investigated using two different methods 1) gillnets for large scale effect of the mussel beds on the fish community (0-100 m) and 2) video observations for small scale effect (0-2 m). Gillnets were deployed at 9 stations in the Control and Impact area with 3 stations at 0-2 m, 2-4 m and 4-6 m depth (*Table 1*). Each station was sampled once a month from May to October *before* and *after* mussel bed establishment, using multi mesh size gillnets. The mesh sizes in the different panels were 6.5, 8.5, 11, 14.3, 18.6, 24.2, 31.4, 40.9, 53.1, 69, 89.7 and 116.6 mm and applied in random order during sampling. Height of the nets were 1.5 m and length was 3 m (mesh size 6.5-14.3 mm), 6 m (mesh size 18.6-40.9 mm), or 12 m (mesh size 53.1-116.6 mm) (Eigaard et al., 2000). All nets were deployed in the afternoon and hauled the following morning. The catch was identified to species level, and total length was measured to the nearest 0.5 cm below and weighed ($\pm$ 1 g wet weight). No differentiation was made between sprat/herring, salmon/trout and common/sand goby.

Two cameras (Sport, LH Camera, Denmark) recorded close-up of the mussel structures in the Impact area and sandy bottom in Control area both at 4-5 m depth (*Table 1*). The cameras recorded continuously for 12 h. All video sampling was carried

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out in late summer *after* mussel bed establishment in five consecutive days. Subsequently, fish appearance was counted for every second minute for the first 10 minutes of each hour. The remaining video sequences were viewed but not analysed. To avoid bias from the deployment operation, the first 30 min after deployment of the camera was omitted.

Development of new method

The local community of recreational fishermen (Danish Organization for Amateur Fishermen in Faaborg) contributed to the project on a volunteer basis and did most of the practical work (i.e. crowdsourcing).

Mussel beds were established in 2010 and 2011 with two different methods. In 2010 blue mussels were produced in a mussel farm on suspended long-lines and harvested from a specialized vessel in November 2010. The harvested mussels were thereafter used to establish mussel beds in the Impact area as described above (*Fig. 2b*). In 2011 blue mussels were produced directly on hemp sacks (100 L) filled with 40 L of shells hung from the long-line system. The mussel beds were then constructed in September 2011 outside the Impact area by transporting the long-line with the hemp bags between two boats to the Impact area. The mussel bags were then detached from the line and allowed to sink to their placement with approximately the same distance between the bags as in 2010. The effect of the second mussel bed establishment 2011 was not investigated.

Table 1. *Samples carried out in 2010 and 2011. For secchi depth, the first number represents the number of samples statistically analysed and the number in parenthesis is the actual number of samples.*

Sampling	2010			2011		
		Impact			Impact	
	Control	Off structure	On structure	Control	Off structure	On structure
Epibenthic sledge	4	6		5	5	
Gillnet	54	54		54	54	
Video obs.				11 h		23 h
Eelgrass cover	701 obs	1201 obs		501 obs	591 obs	
Secchi depth	0 (31)	0 (30)		14 (99)	14 (106)	11 (22)

Data analysis and statistics

Secchi depth: The difference between average secchi depths was analysed in the Control area, Impact area and directly on the mussel bed area in 2011. Only averages on days where secchi depth was measured in all 3 areas or minimum in Control and Impact area were included in the analyses to ensure that the differences were caused by area and not by time. Data was tested using a GLM (model: area + day) where area was either Control or Impact and day was a random effect.

Eelgrass: The difference in eelgrass coverage was tested at 4-6 m depth (mussel bed establishment depth) with logistic regression. The independent variable in the model was eelgrass coverage with category values between 0 to 4 while the dependent variables were areas (Control, Impact) and years (2010 (*before*), and 2011 (*after*)).

Epibenthic Samples: Using the BACI design (Underwood 1992) ensured that any

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detected changes found were a result of the establishment of blue mussel beds and not temporal or spatial variability. Standardized cross effect of Control-Impact and *before-after* was estimated by LSmean function in proc-GLM (model: Year*Area). Abundance data were log-transformed. The following variables were used: year (2010 and 2011), area (Control and Impact) and species.

Fish Community: Standardized cross effect of BACI was estimated by LSmean function in proc-GLM (Abundance model: Year*Area). Abundance data were log-transformed. The following variables were used: year (2010 and 2011), area (Control and Impact), species (the most dominant species was analysed separately while the remaining species were grouped into “Other species”), depth (0-2 m, 2-4 m and 4-6 m), low/high impact area (0-4 m and 4-6 m) and season (May+Jun, Jul+Aug and Sep+Oct).

The abundance of fish pr. video sequence followed a negative binomial distribution and data was analysed for any effects of area and time of day by LSmean function in proc-GLM (abundance = area month hour). Data were log-transformed and observations were divided into morning (8:00-11:00), noon (12:00-15:00) and evening (16:00-19:00).

The threshold for rejection of the null hypothesis was defined as P=0.05. Data was statistically analysed in SAS 9.4.

Results

Establishment of blue mussel beds

The naturally occurring blue mussel beds in Nørrefjord were generally in poor condition consisting primarily of empty, crushed shells and very few live mussels. The natural beds were small (<5-7 m in diameter) and occurred mainly from 4-6 m. Therefore the produced blue mussels were established in beds to imitate the size and placement of natural mussel beds in other areas of Nørrefjord: 1-2 m diameter spaced 3-10 m apart at 4-6 m depth corresponding to 121.000 m^2 of mussel bed in total (*Fig. 2A*).

A rough estimate based on diver and video observations showed that approximately 5% of the mussels had survived until spring of 2011. The structures of the beds were intact as the empty mussel shells still remained on the fjord bottom.

Fish communities

A total of 19 different fish species were caught in gillnets in 2010 and 15 in 2011. In both years the catches were dominated by three species: cod (*Gadus morhua*) black goby (*Gobius niger*) and three-spined stickleback (*Gasterosteus aculeatus*), which combined accounted for 81% of the total catches. The statistical tests focused on these three species, as all other species occurred in low numbers (*Table 2*) and were combined in the category “Other species” for statistical testing.

On the video recordings 112 primarily smaller fish were observed in both areas in 2011. Seven taxonomical groups were recorded (*Table 2*) and goby was the most common group represented by black, sand and undetermined goby comprising approximately 66% of the observations in the Impact area. Undetermined species comprised 29% of the catches but was most likely from the G*obiidae* family. Only one fish species was observed in the Control area and four species were observed in the Impact area, disregarding the goby sp. and unidentified fish species.

A significant cross effect on fish abundance of year and area, i.e. a direct effect of mussel bed establishment was only found for black goby at 0-4 m depth (P=0.004 – se all P-values in *Table 3*). The mean abundance of black goby decreased from 4.7 to 0.2 ind. day^{-1} in the Control area and from 5.2 to 0.02 ind. day^{-1} in the Impact area from 2010 to 2011.

Yearly variation in abundance was significant for cod, black goby and three-spined stickleback in both 0-4 m depth and 4-6 m depth (all $P<0.05$), with an increase in cod and three-spined stickleback and decrease in black goby from 2010 to 2011. A significant effect of area was only observed for black goby (P=0.009). Significant changes in abundance caused by season were observed for cod in the 4-6 m depth and black goby in 0-4 and 4-6 m depth (*Fig. 3*). For all other fish species no significant changes were observed for any of the analysed variables.

Table 2. *Abundance of fish species caught in gillnets and observed in video observations in the Control and Impact area.*

Scientific name	Gillnet catch pr. day n	Gillnet catch pr. day n	Video obs pr. day n	Video obs pr. day
	Control n=108	Impact n=108	Control 11 h	Impact 23 h
Agonus cataphractus	0.3			
Ammodytes tobian	1.7	1.8		
Belone belone	2.0	0.5		
Ctenolabrus rupestris				5.2
Eutrigla gurnardus		0.2		
Gadus morhua	48.2	50.7		
Gasterosteus aculeatus	109.3	149.2		
Gobius niger	69.7	51.7		25
Merlangius merlangus	0.2			
Myoxocephalus scorpius	13.0	26.7		
Pholis gunellus	0.2			
Platichthys flesus	3.3	2.5		
Pleuronectes platessa	0.3	0.5		
Pomatoschistus minutus/microps	6.3	4.8		7.3
Salmo salar/trutta	2.5	0.7		
Scomber scombrus	3.5	4.5		
Spinachia spinachia	9.0	4.0		
Sprattus sprattus/Clupea harengus	12.5	4.7		
Syngnathus typhle		0.2	17.5	
Zoarces viviparus	6.7	16.7		1
*goby				51.1
Undetermined			24	36.5
Total	**288.7**	**319.2**	**41.5**	**126.1**

There was a highly significant difference between the abundance of fish observed on video ($P<0.0001$) in the Impact area compared to the Control area, with three times as many fish observed directly on the mussel beds (*Table 2*). In addition to this, a diel variation occurred, as significantly more fish were observed in the morning compared to

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noon and evening (P<0.0001). There was no significant difference between noon and evening (P=0.19).

Outside the processed 5x2 minute observations, cod, trout and flatfish were observed on several occasions but only in the Impact area.

Epibenthic samples

In total, 14 taxa were recorded in epibenthic samples of which 9 were identified to species level (*Table 4*). Two of the taxa were fish (*Sygnathus typhle* and *Pomatochistus microps*) and one was blue mussel (*Mytilus edulis*). All three were omitted from the analysis leaving 11 taxa of benthic invertebrates in the analysis. Crustaceans dominated the community both in terms of numbers and taxa with 8 of the 11 invertebrate taxa.

Table 3. *P-values for mean abundance of fish caught in gillnets. Significance levels are set at: * 0.05, ** 0.01, *** 0.001. The ÷ for Gobius niger in Year*Area column at 0-4 m depth indicate that the cross effect of year and area was significantly negative for this species.*

Abundance	Impact	Year	Area	Year*Area	Season	Depth
Gadus morhua	High (4-6 m)	***	P=0.2	P=0.1	P=0.8	-
	Low (0-4 m)	***	P=0.7	P=0.5	**	P=0.07
Gobius niger	High (4-6 m)	***	P=0.1	P=0.1	***	-
	Low (0-4 m)	***	**	÷ **	***	P=0.8
Gasterosteus aculeatus	High (4-6 m)	*	P=0.4	P=0.5	P=0.3	-
	Low (0-4 m)	**	P=0.8	P=0.7	P=0.09	*
Other	High (4-6 m)	P=0.9	P=0.4	P=0.6	P=0.07	-
	Low (0-4 m)	P=0.8	P=0.1	P=0.6	P=0.4	P=0.06

Only one species in each of the taxonomical phylums Echinodermata, Annelida and Urochordata was found.

In general, year and area had an effect on abundance of most species of epibenthos. A positive significant effect of mussel beds on abundance was found for Polynoidae (P=0.04), *Praunus flexuosus* (P=0.04) and *Idotea baltica* (P=0.006) (cross effect of year and area) (*Table 4*). The abundance of *Idotea* increased only in the Control area, so the effect of mussel beds in the Impact area seems to be negative for this species. No significant effect of mussel beds was observed for all species suited as fish prey (all species except tunicate (*Ascidiae*) and starfish (*Asterias rubens*)) or all species combined.

Starfish increased 15 to 32 fold in the Impact and Control area, respectively, from 2010 to 2011. All starfish were relatively small ranging from 4 mm to 9 cm with 70% measuring < 15 mm.

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Table 4. *Abundance of epibenthic invertebrates m^{-2} in the Control and Impact area before (late October 2010) and after (early November 2011) mussel bed establishment. "-" signifies too few observations for statistical analysis. Significance levels are set at: * 0.05, ** 0.01, *** 0.001.*

Benthic invertebrates	**2010 No m^{-2} Control n=4**	**2010 No m^{-2} Impact n=6**	**2011 No m^{-2} Control n=5**	**2011 No m^{-2} Impact n=5**	**Fish prey**	**Significant changes Year**	**Area**	**Year*Area**
Crustacea								
Corophiidae	1.2	2.3	0.3	4.7	Yes		**	
Crangon crangon	0.9	5.7	1.6	3	Yes			
Gammaridae	2	1.4	0.3	20.1	Yes			
Idotea baltica	0.1	2.8	17.4	3.3	Yes	***		***
Ostracoda	0	0	0	0	Yes	-	-	-
Palaemon adspersus	2.3	2	0.3	0	Yes	**		
Phtisica marina	0	0	0.3	9.6	Yes	***		
Praunus flexuosus	0.5	0.1	6.7	18.6	Yes	***		*
Echinodermata								
Asterias rubens	0.7	2.2	26.9	28.3	No	***		
Annelida								
Polynoidae	0.1	0	0.9	3.1	Yes	**		*
Urochordata								
Ascidacea	0	0.1	1	0.4	No	***		
n total	**8**	**16.5**	**55.9**	**91.3**		***		
n fish prey	**7.3**	**14.2**	**28**	**62.5**		**		

Eelgrass and water quality

All secchi measurements varied between 3.4 and 6.0 m with slightly deeper measurements during early summer compared to late summer as could be expected due to seasonal variation in planktonic blooms (data not shown). No significant difference was found between the Control and Impact area ($P=0.36$).

The restored mussel beds did not affect eelgrass coverage significantly when comparing eelgrass coverage in the Control area and Impact area in 2010 or 2011 ($P>0.05$, logistic regression). Neither were there significant differences when comparing areas with and without restored beds in the Impact area at 4-6 m depth ($P>0.05$, Chi-Square test). Depth was the only factor that had a significant effect on eelgrass coverage ($P<0.0001$, Chi-Square test). Video observations of eelgrass cover showed dense mats until 4-5 m depth and a maximum depth of 7.4 m in both the Control and Impact area.

Development of new method

In 2010 the mussels were produced on suspended long-line systems. Based on mussel coverage, weight and long-line length in the mussel farm, it was estimated that a total of 28 tons of blue mussel were produced in 2010. The harvest and subsequently construction of mussel beds was labour-intensive and 14 men and 5 boats worked for 8 days.

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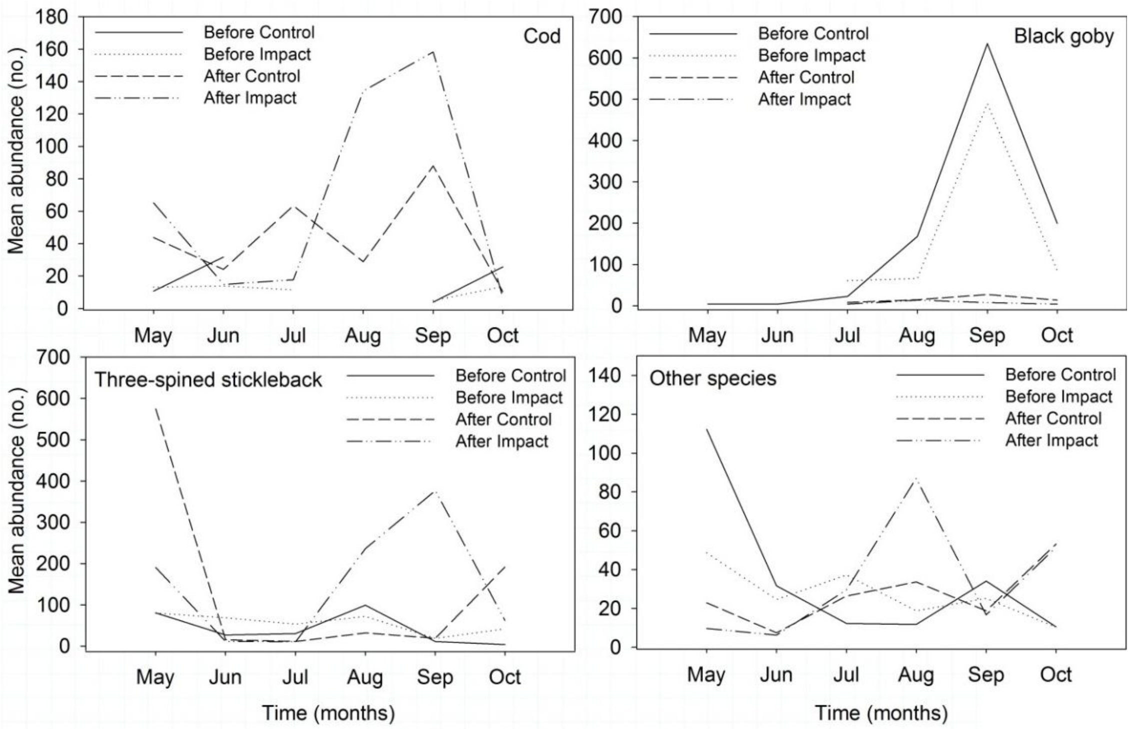

Figure 3. *Monthly (May-Oct) fish catches for cod, black goby, stickleback and other species caught in gillnets in the Control and Impact area before and after mussel bed establishment. Notice the difference in abundance between species.*

To reduce the work load in the harvest process, blue mussels were in 2011 produced on hemp sacks on the long-lines. It was estimated that 16 tons of blue mussels were produced using this method. The harvest and construction of mussel beds required 12 men and 5 boats in 1 day.

Discussion

Effect of mussel bed establishment

The mussel bed structures improved fish habitat on a local scale resulting in a higher abundance and biodiversity of fish directly on the introduced mussel structures. In particular, small gobies were observed circling around the structures for extended periods. Similar observations were made around stone reefs and wind turbine foundations in the Baltic Sea where gobies were observed to occur in significantly higher numbers within a few meters from the structures (Wilhelmsson et al., 2006; Andersson and Öhman, 2010; Hansen, 2012). Also larger fish (e.g. cod) are known to be surprisingly stationary (Lindholm et al., 2007; Karlsen, 2011). The very local effect of structures could explain why the effect of the established mussel beds in the present study was greatest in the video observations rather than the larger scale gillnets and epibenthic sledge.

Very few mussels survived the starfish predation, but the structure remained intact as empty shells. The increase in starfish abundance in spring 2011 could not be related to the establishment of the mussel beds as the increase in starfish abundance occurred both in the Control and Impact area. High abundance of starfish was also reported from adjacent waters (Lille Belt) (pers. com. Allan Buch). The structures comprised by the empty mussel shells are reported to be just as important as live mussels as they still function as shelter for associated fauna (Palomo et al., 2007; Norling and Kautsky, 2007). In this study, the persistence of the local effect on fish abundance and biodiversity, despite the high predation rate by starfish on the blue mussels, supports the finding that the fish habitat function of the mussel bed remains intact with its structure, despite the loss of live blue mussels.

Gobies are mesopredators and attract larger piscivorous species, such as cod and trout (Fjøsne and Gjøsæter, 1996; Wennhage and Pihl, 2002; Almqvist et al., 2010). The observation of large piscivorous species (trout and cod) in the Impact area suggests that the same attraction mechanism was present around the established mussel bed structures. There was a tendency towards increased cod abundance after mussel bed establishment (*Fig. 3).* This increase in predation pressure could explain the decreased black goby abundance. We did not see the same decrease for three-spined stickleback. This may be due to the relatively large spines of the stickleback that make it a less attractive prey compared to the goby (Wennhage and Pihl, 2002).

The goldsinny wrasse (*Ctenolabrus rupestris*) is a fish species occurring in higher densities near rocky substrates and exhibits high affinity to these types of complex habitats (Gjøsaeter, 2002). The presence of goldsinny wrasse on the established mussel structures suggest that the mussel structure provided a complex habitat similar to rocky reefs that could attract this reef-associated species.

Eelgrass and water quality

The establishment of the mussel bed in the present study did not affect the eelgrass coverage or depth range. Eelgrass cover was generally in good condition in Nørrefjord with patches as deep as 7-8 m in depth. The reason for the good condition in Nørrefjord is probably the reduced nitrogen loading compared to the 1980s (data, The Danish Natural Environment Portal, miljoeportal.dk, Rask et al., 2000). The decrease in nitrogen loading has gradually increased the secchi depth (data, The Danish Natural Environment Portal, miljoeportal.dk) and improved the light conditions for eelgrass.

An effect on secchi depth after the establishment of the new mussel beds could not be expected due to the magnitude of the established mussel beds. A conservative estimate of potential filtration rate with 5% survival of the 28 tons mussels established in beds in autumn 2010 would be 5600 m^3 d^{-1} (based on filtration rate for 25 mm blue mussels found by Winter, 1973). The total body of water in Nørrefjord is 213 x 10^6 m^3 and according to maximum tidal amplitude, the exchanged body of water is estimated to 15.6 x 10^6 m^3 twice a day, not taking into account any wind effect. Thus, even if all the mussels had survived, the filtration rate would have been 0.1 x 10^6 m^3 and still not enough to filter the water body exchanged by the tide alone. However, other studies have demonstrated a depletion of phytoplankton around blue mussel long-line systems with up to 80% and up to 1.5 m increase in secchi depth (Petersen et al., 2013). It has been estimated that an increase in secchi depth of 12 cm in Skive Fjord (another Danish fjord resembling Nørrefjord in area and mean depth) could be achieved by 18.8 ha of mussels on suspended long-lines (Petersen et al., 2013). That is 13 times larger than the mussel farm used in Nørrefjord. As bottom living mussels experience depletion of food items due to less exchange of water near the bottom compared to suspended mussels (Petersen et al., 2013), Nørrefjord would need even more mussels and thus a larger

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proportion of the fjord bottom, to see the same change as for the suspended mussels studied in Skive Fjord. However, since an increase in secchi depth would in time increase macro algae and eelgrass depth range (Nielsen et al., 2002) the establishment of mussel beds in these areas may be one way to improve local environmental conditions in semi-enclosed fjords.

Development of a new method

The method with mussel production on hemp sacks on the long-lines followed by direct establishment of the mussel beds was the most effective method both in time and labour compared to the traditional long-line system. The hemp sack method can be applied to many other geographic locations. The heavy involvement of local volunteers can be recommended in future ecological improvement- and restoration projects. Crowdsourcing allowed us to conduct the experiment cost-effectively. As long as the projects evolve in collaboration with researchers and local managers, this development of bottom-up initiated projects may be beneficial to society and increase environmental awareness of the local community (Grese et al., 2000). The increased awareness was reflected in the wide interest in the project from local and regional newspapers, radio stations as well as the attendance at stakeholder meetings (Assens Municipality, Developing Fyn Municipal Ltd (Lag Fyn), The Danish Nature Agency of Odense, the Danish Ministry of the Environment and local interest organizations such as the sailing club and the Danish Organization for Amateur Fishermen). It was even suggested by the stakeholders that this collaboration with the local community should be best practice in all future habitat restoration projects.

Conclusions

In conclusion, this study showed that it was possible to improve fish habitats on a local scale. The blue mussel structures established in Nørrefjord improved shelter and food especially for small mesopredator fish. The quantity of blue mussels established in Nørrefjord was insufficient to observe any effect on secchi depth and eelgrass cover and range. A new method was introduced, as we succeeded to establish mussel beds in a cost-effective way using crowdsourcing (local volunteer fishermen). The hemp sacks attached to the long-lines proved to be the most effective method of the two methods tested.

This study shows that with the help of volunteers, this habitat improvement strategy is a potential useful management tool to increase fish abundance and improve fish communities in Danish fjords in the future. Therefore, we recommend more local involvement in future improvement and restoration projects.

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REFERENCES

[1] Ærtebjerg, G., Andersen, J.H., Hansen, O.S. (eds) (2003): Nutrients and eutrophication in Danish marine waters. A challenge for science and management. Scientific Report. National Environmental Research Institute, Ministry of the Environment. Denmark.

[2] Airoldi, L., Beck, M.W. (2007): Loss, status and trends for coastal marine habitats of Europe. – In: Gibson, R., Atkinson, R.J.A., Gordon, J.D.M. (eds) Oceanography and marine biology: An annual review 45: 345–405.

[3] Almqvist, G., Strandmark, A.K., Appelberg, M. (2010): Has the invasive round goby caused new links in Baltic food webs? – Environmental Biology of Fishes 89: 79–93.

[4] Andersson, M.H., Öhman, M.C. (2010): Fish and sessile assemblages associated with wind-turbine constructions in the Baltic Sea. – Marine and Freshwater Research 61: 642–650.

[5] Bryant, D., Rodenburg, E., Cox, T., Nielsen, D. (1995): Coastlines at risk: an index of potential development-related threats to coastal ecosystems. – WRI Indicator Brief, World Resources Institute , Washington, DC.

[6] Carbines, G., Jiang, W., Beentjes, M.P. (2004): The impact of oyster dredging on the growth of blue cod, Parapercis colias, in Foveaux Strait, New Zealand. – Aquatic Conservation: Marine and Freshwater Ecosystems 14: 491–504.

[7] Christiansen, T., Christensen, T.J., Markager, S., Petersen, J.K., Mouritsen, L.T. (2006): Limfjorden i 100 år. Klima, hydrografi, næringsstoftilførsel, bundfauna og fisk i Limfjorden fra 1897 til 2003. Scientific Report no. 578. National Environmental Research Institute, Denmark. In Danish.

[8] Dolmer, P., Christensen, H., Hansen, B., Vismann, B. (2012): Area-intensive bottom culture of blue mussels Mytilus edulis in a micro-tidal estuary. – Aquaculture Environment Interactions 3: 81–91.

[9] Dolmer, P., Frandsen, R. (2002): Evaluation of the Danish mussel fishery: suggestions for an ecosystem management approach. – Helgoland Marine Research 56: 13–20.

[10] EEA (1999): Environment in the European Union at the turn of the century. State of environment report, 1/1999. European Environment Agency. Copenhagen, Denmark.

[11] Eigaard, O.R., Støttrup, J., Hovgård, H. (2000): Udvikling af standard garnserie til brug ved rutinemæssig bestandsanalyse af flad- og rundfisk i marine lavvandede områder. Scientific report no. 78. Danish Institute for Fisheries Research. Charlottenlund, Denmark. In Danish.

[12] Fjøsne, K., Gjøsæter, J. (1996): Dietary composition and the potential of food competition between 0-group cod (Gadus morhua L.) and some other fish species in the littoral zone. – ICES Journal of Marine Science 53: 757–770.

[13] Gjøsaeter, J. (2002): Distribution and density of goldsinny wrasse (Ctenolabrus rupestris) (Labridae) in the Risør and Arendal areas along the Norwegian Skagerrak coast. – Sarsia 87: 75–82.

[14] Grese, R.E., Kaplan, R., Ryan, R.L., Buxton, R. (2000): Psychological benefits of volunteering in stewardship programs. – In: Gobster, P.H., Hull, B. (eds) Restoring nature: perspectives from the social sciences and humanities. Island Press, Wahington D.C., p 265-280.

[15] Hansen, K.S. (2012): Small scale distribution of fish in offshore wind farms. Master thesis report in Biology. University of Copenhagen and Technical University of Denmark, Charlottenlund, Denmark.

[16] Heck, K.J., Wetstone, G. (1977): Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. – Journal of Biogeography 4: 135–142.

[17] Holm, P. (2005): Human impacts on fisheries resources and abundance in the Danish Wadden Sea, c1520 to the present. – Helgoland Marine Research 59: 39–44.

[18] IPCC (2014): Climate Change 2014. Fifth Assessment Synthesis Report. Intergovernmental Panel on Cliamte Change. Copenhagen, Denmark.

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: 10.15666/aeer/1303_783798

[19] Jones, D., Clare, J. (1977): Annual and long-term fluctuations in the abundance of fish species inhabiting an intertidal mussel bed in Morecambe Bay, Lancashire. – Zoological Journal of the Linnean Society 60: 117–172.
[20] Kaiser, M., Clarke, K., Hinz, H., Austen, M., Somerfield, P., Karakassis, I. (2006): Global analysis of response and recovery of benthic biota to fishing. – Marine Ecology Progress Series 311: 1–14.
[21] Karlsen, J.D. (2011): Hot on the tail of hefty Atlantic cod: an interdisciplinary study on the behaviour at ship wrecks in the North Sea. Dissertation. Aarhus University and Technical University of Denmark. Denmark.
[22] Krause-Jensen, D., Carstensen, J., Nielsen, S.L., Dalsgaard, T., Christensen, P.B., Fossing, H., Rasmussen, M. (2011): Sea bottom characteristics affect depth limits of eelgrass Zostera marina. – Marine Ecology Progress Series 425: 91–102.
[23] Krause-Jensen, D., Markager, S., Dalsgaard, T. (2012): Benthic and pelagic primary production in different nutrient regimes. – Estuaries and Coasts 35: 527–545.
[24] Lindholm, J., Auster, P., Knight, A. (2007): Site fidelity and movement of adult Atlantic cod Gadus morhua at deep boulder reefs in the western Gulf of Maine, USA. – Marine Ecology Progress Series 342: 239–247.
[25] Luckhurst, B.E., Luckhurst, K. (1978): Analysis of the influence of substrate variables on coral reef fish communities. – Marine Biology 49: 317–323.
[26] Mackenzie, C.L., Lynch, S.A., Culloty, S.C., Malham, S.K. (2014): Future oceanic warming and acidification alter immune response and disease status in a commercial shellfish species, Mytilus edulis L. – PloS One 9 (6): e99712
[27] McDermott, S., Burdick, D., Grizzle, R., Greene, J. (2008): Restoring ecological functions and increasing community awareness of an urban tidal pond using blue mussels. – Ecological Restoration 26: 254–262.
[28] Nelson, W.G., Bonsdorff, E. (1990): Fish predation and habitat complexity: are complexity thresholds real? – Journal of Experimental Marine Biology and Ecology 141: 183–194.
[29] Newell, R., Koch, E. (2004): Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. – Estuaries 27: 793–806.
[30] Nielsen, T., Maar, M. (2007): Effects of a blue mussel Mytilus edulis bed on vertical distribution and composition of the pelagic food web. Marine Ecology Progress Series 339: 185–198
[31] Nielsen, P.E., Petersen, E.H. (2013): Råstofproduktion i Danmark. Havområdet 2012. Scientific Report. Nature Agency, Danish Ministry of the Environment, Copenhagen, Denmark. In Danish.
[32] Nielsen, S.L., Sand-Jensen, K., Borum, J., Geertz-Hansen, O. (2002): Depth colonization of eelgrass (Zostera marina) and macroalgae as determined by water transparency in Danish coastal waters. – Estuaries 25: 1025–1032.
[33] Norling, P., Kautsky, N. (2007): Structural and functional effects of Mytilus edulis on diversity of associated species and ecosystem functioning. – Marine Ecology Progress Series 351: 163–175.
[34] Norling, P., Kautsky, N. (2008): Patches of the mussel Mytilus sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. – Aquatic Biology 19: 75–87.
[35] Palomo, M., People, J., Chapman, M., Underwood, A. (2007): Separating the effects of physical and biological aspects of mussel beds on their associated assemblages. – Marine Ecology Progress Series 344: 131–142.
[36] Petersen, J., Maar, M., Ysebaert, T., Herman, P. (2013): Near-bed gradients in particles and nutrients above a mussel bed in the Limfjorden: influence of physical mixing and mussel filtration. – Marine Ecology Progress Series 490: 137–146.
[37] Petersen, J.K., Timmermann, K., Holmer, M., Hasler, B.E., Cordula, G., Marianne, Z. (2013): Miljømuslinger. Muslinger som supplerende virkemiddel. Notat fra DCE -

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: 10.15666/aeer/1303_783798

Nationalt Center for Miljø og Energi. Scientific Report. University of Aarhus and Danish Nature Agency, Danish Ministry of the Environment. Denmark. In Danish.

[38] Peterson, C., Grabowski, J., Powers, S. (2003): Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. – Marine Ecology Progress Series 264: 249–264.

[39] Pihl, L., Modin, J., Wennhage, H. (2005): Relating plaice (Pleuronectes platessa) recruitment to deteriorating habitat quality: effects of macroalgal blooms in coastal nursery grounds. – Canadian Journal of Fisheries and Aquatic Sciences 62: 1184–1193.

[40] Rask, N., Madsen, H.B., Larsen, S. (2000): Vandmiljøovervågning. Kystvande 1999. Miljø- og Arealafdelingen og Natur og Vandmiljøafdelingen, Fyns Amt. Scientific Report. Odensen, Denmark. In Danish.

[41] Riemann, B., Nielsen, T., Horsted, S., Bjørnsen, P., Pock-Steen, J. (1988): Regulation of phytoplankton biomass in estuarine enclosures. – Marine Ecology Progress Series 48: 205–215.

[42] Seitz, R.D., Wennhage, H., Bergström, U., Lipcius, R.N., Ysebaert, T. (2014): Ecological value of coastal habitats for commercially and ecologically important species. – ICES Journal of Marine Science 71: 648–665.

[43] Sundblad, G., Bergström, U., Sandström, A., Eklöv, P. (2014): Nursery habitat availability limits adult stock sizes of predatory coastal fish. – ICES Journal of Marine Science 71: 672–680.

[44] Underwood, A.J. (1992): Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. – Journal of Experimental Marine Biology and Ecology 161: 145–178.

[45] Wennhage, H., Pihl, L. (2002): Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. – Journal of Fish Biology 61: 207–228.

[46] Wilhelmsson, D., Yahya, S.A.S., Öhman, M.C. (2006): Effects of high-relief structures on cold temperate fish assemblages: A field experiment. – Marine Biology Research 2: 136–147.

[47] Winter, J.E. (1973): The filtration rate of Mytilus edulis and its dependence on algal concentration, measured by a continuous automatic recording apparatus. – Marine Biology 22: 317–328.

[48] Wulff, F., Humborg, C., Andersen, H.E., Blicher-Mathiesen, G., Czajkowski, M., Elofsson, K., Fonnesbech-Wulff, A., Hasler, B., Hong, B., Jansons, V., Mörth, C.M., Smart, J.C.R., Smedberg, E., Stålnacke, P., Swaney, D.P., Thodsen, H., Was, A., Zylicz, T. (2014): Reduction of Baltic Sea nutrient inputs and allocation of abatement costs within the Baltic Sea catchment. – Ambio 43: 11–25.

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Paper II

Restoration of a temperate reef: Effects on the fish community

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Scientific Research

Restoration of a Temperate Reef: Effects on the Fish Community

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Abstract

The extraction of large boulders from coastal reefs for construction of harbours and coastal protection has led to habitat degradation for local fish populations through the destruction of cavernous reefs and changes in macroalgal cover resulting from a loss of substrate. The temperate reef at Læsø Trindel in Kattegat, Denmark, has now been re-established with the aim of restoring the reef's historical structure and function. The effects of the restoration on the local fish community are reported here. Fishing surveys using gillnets and fyke nets were conducted before the restoration (2007) and four years after the restoration of the reef (2012). Species of the family Labridae, which have a high affinity for rocky reefs, dominated both before and after the restoration. Commercially important species such as cod *Gadus morhua*, and saithe *Pollachius virens*, occurred infrequently in the catches in 2007 but were significantly more abundant in the catches in 2012. Cods were especially attracted to the shallow part of the reef that was restored by adding stones. For some species, such as ballan wrasse *Labrus bergylta*, and cod, the proportion of larger individuals increased after the restoration. The findings highlight the importance of reef habitats for fish communities and the need for their protection.

Keywords

Reef Restoration, Impact Analysis, Labridae, Gadidae

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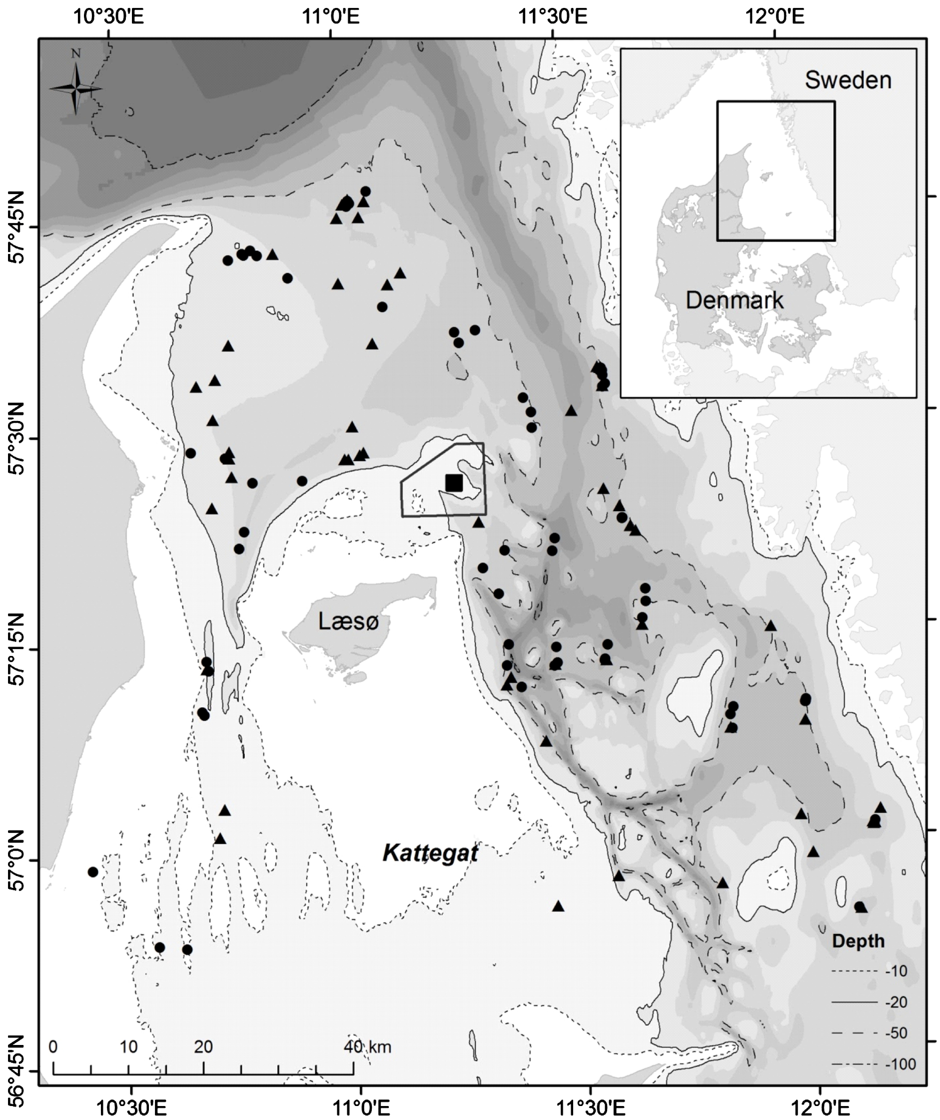
1. Introduction

Marine reefs are important fish habitats providing complex structures that provide refuge for fish and hard substrate for benthic fauna and macroalgal forests that provide refuge and feeding sites for fish [1]-[3]. Reefs are listed in the EU Habitats Directive (1170 Reefs; Council Directive 92/43/EEC) and, for this reason, marine reefs in Danish waters have been designated as protected areas and are part of the EU-wide Natura2000 network indicating the acknowledged importance of this habitat type. Most of our knowledge on reef habitats is derived from studies on tropical reefs, although in the recent decade more focus has been directed towards the quantitative significance for fish communities of reef habitats in temperate areas. Most monitoring for fish assessment is limited to relatively smooth bottom areas due to the design of the survey gear [4]. Monitoring of fish communities on complex habitats such as temperate reefs and biogenic reefs are often limited to specific ecological studies of limited duration [5] [6]. Significantly higher catch rates of cod *Gadus morhua* on rough than on smooth bottom were suggested to be the main source for underestimation of the stock size of the North Sea cod [7]. Thus, limited temporal knowledge is available on the fish diversity and abundance in relation to temperate reefs and the quantitative ecological role of temperate reefs in our region.

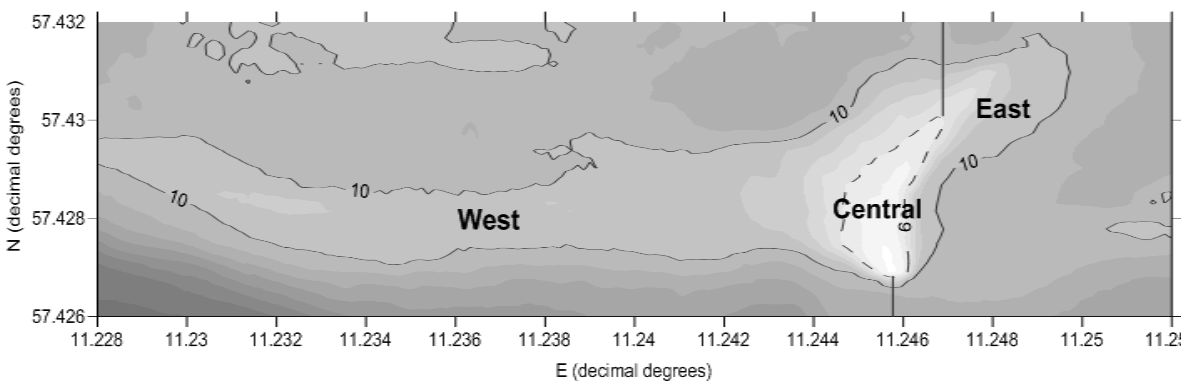
Extensive mineral extraction of stones and boulders in coastal areas of Denmark [8] has not only led to destruction of cavernous reefs and removal of hard bottom but also removal of biogenic structures associated with these reefs and which are a main feature of temperate reefs [9]. The removal of larger boulders increases the average depth which may result in reduced benthic plant growth due to reduced light penetration with depth. A reduction of benthic plant growth reduces habitat complexity and reduces type and diversity of refugia for juvenile fish. The removal of the top stabilizing layer of larger boulders may also result in destabilization of the remaining reef, where smaller boulders or stones may be upturned in storms or strong current events with subsequent loss of perennial macrophytes and potential colonization of opportunistic macroalgal species. In Denmark, mineral extraction of large stones has now ceased but the consequences of the historical removal of material and destruction of these habitat types for fish populations are largely un-documented. No archives are available on the magnitude or precise geographic locations of the extractions.

The reef at Læsø Trindel, north-east of the island Læsø in Kattegat, Denmark (**Figure 1(a)**) was one of the many reef areas where mineral extractions took place during a period in the last century [8]. Archival maps showed the shallowest part of the reef to be 1.25 m below the surface in 1831. The depth increased to 2.2 m in 1930 and to ~4 m in the 1970s [10]. No information is available on how many boulders were mined from this reef complex. The macroalgal vegetation at this site was included in the National Marine Monitoring Program in 1991 and the results of the monitoring showed that the status of the reef was not in a Good Environmental State mainly due to the high dominance of opportunistic species at the expense of perennial species, compared to other sites in the monitoring program [11].

Species of the Labridae family are likely to be most affected by loss of reef habitats because of their high affinity to these habitat types and their complete dependence on this substrate for recruitment [12]. In fact, these authors suggested that a good indicator for the status of this habitat type might be the abundance of Labridae species or proportion of larger fish of Labridae as they depend on this substrate for reproduction. These species are, however, of no commercial value and are, therefore, not monitored. Thus, changes in their abundance or distribution may go undetected. In rocky habitats, species of Labridae also serve as prey for commercially important piscivors such as cod, mackerel *Scombrus scombrus*, saithe *Pollachius virens*, and whiting *Merlangius merlangus* that rely on teleosts as a major food source [13]. Thus, loss or degradation of rocky habitats may result in changes in trophic dynamics and impact trophic integrity in and around these habitat types. In recent decades, habitat restoration has expanded from terrestrial areas to the aquatic environment. In the aquatic environment, focus has been on freshwater systems (e.g. [14]). Restoration efforts in the marine environment are diverse, most of which have focused on restoring coral reefs [15], or large structural elements such as planting vegetation [16], restoring mangroves [17] and oyster reefs [18]. Unlike impacts from other human activity such as eutrophication and fishing, where the removal of the cause of the impact may lead to system recovery, reef habitats cannot be expected to recover without human intervention. The restoration of the marine temperate reef at Læsø Trindel (Kattegat, Denmark) represents one such large-scale intervention in European waters to restore a degraded natural reef. To our knowledge, this study represents the first temperate reef restoration in European waters. Although we have no details on the original form of the reef, we can use "before" and "after" restoration studies of biodiversity distributions on the reef to infer how reef damage affects ecosystems. In this study, the



(a)



(b)

Figure 1. (a), (b) Map of the location of the reef at Læsø Trindel (black square, **Figure 1(a)**) within the NATURA 2000 site in the Kattegat (black border). Black circles (2005-2007; BEFORE) and triangles (2010-2012; AFTER) mark the positions of the stations from the research trawl surveys within 50 km of the reef site. **Figure 1(b)** shows the actual reef studied with 6 and 10 m depth contours and the location of the three sampling areas.

damaged reef was restored to its former function in 2008 to serve as substrate for larger kelp-forming algae.

The aim of this study was to examine whether effects of restoring the boulder reef could be identified for the associated fish community. Effects on bottom fauna and flora of the reef restoration are presented elsewhere [10]. We hypothesized that the reef after restoration would provide more refugia and higher prey abundance than prior to restoration and that this would favor a higher abundance of reef fishes, a higher species richness and broader size distribution of fish.

2. Materials and Methods

2.1. Study Site and Reef Restoration

The reef at Læsø Trindel is located about 12 km north-east of the island of Læsø in the Kattegat (**Figure 1(a)**). The reef was stabilized with a layer of large boulders ranging in individual weight from 1600 kg to 3300 kg and parts of the central reef area were restored to its original depth during 2008 (**Figure 1(b)**; [19]). A total of ~100,000 tons of boulders originating from Norway were deployed, covering an area of ~27,600 m^2 distributed in the depth range of 4 - 10 m.

2.2. Sampling

The monitoring program was based on a "Before-After" approach. Due to economic constraints only one sampling was conducted before deployment of the reef in June 2007, and one sampling four years after deployment in June 2012. The sampling was a random stratified design. The area on Læsø Trindel was stratified into the areas; the central shallow part of the reef at 2 - 6 m depth, the western central part at 6 - 10 m depth; the eastern central part also at 6 - 10 m depth, and the surrounding area shallower than 10 m (**Figure 1(b)**). Although the depth contours had changed in the area of the restored reef [19], the area stratifications were maintained within the three areas. Fish abundance was surveyed with multi-meshed gillnets [20] and fyke nets. The mesh sizes in the multi-meshed gillnets were 11, 14, 19, 24, 31, 41, 53 and 70 mm. Each panel was 1.5 m high and 6 m in length, except for the 53 and 70 mm panels which were, respectively, 12 m and 52 m long. Each gillnet had a random combination of panels, separated from each other by 1.8 m (float and sink line). The gillnets were deployed in the afternoon or evening and retrieved the following morning resulting in ~12 h fishing time. The fyke nets had a mesh size of 18 mm and were 42 cm in height with a 6.5 m leader. Five fyke nets were mounted together in a row. These were deployed in the afternoon and fished ~48 h. In 2007, 4 replicates were made in each sampling site with gillnets and 7 - 9 replicates with fyke nets. In 2012, 4 - 11 replicates were made with gillnets and 2 - 4 replicates with fyke nets. Catches were identified to species and total length of each fish measured to the nearest lower 0.5 cm and weighed. For gillnets, catch per unit effort (CPUE) was standardized as catch in numbers per species or group per gillnet length in all the combined mesh size panels in the gillnet deployment. For fyke nets, CPUE was standardized as total catch in numbers per species or group for each deployment of the combined five fyke nets.

As we had no control area for monitoring, due to economic constraints, we chose to compare the development in cod abundance BEFORE and AFTER on Læsø Trindel with CPUE data from research trawl surveys in the neighboring area (**Figure 1(a)**). The CPUE provides an index where it is possible to observe positive or negative changes in abundance for each gear type. The trawl surveys are conducted by DTU Aqua in spring and autumn each year. The data from these surveys is also used in stock assessment of cod in the Kattegat in ICES where additional information on the surveys can be found (e.g. [21]). We included data within a distance of 50 km to Læsø Trindel and CPUE was divided into cod smaller or larger than 30 cm total length, and two periods representing the periods BEFORE (year 2005-2007) and AFTER (year 2010-2012). The stations for the trawl sampling are shown in **Figure 1(a)**.

2.3. Data Analyses and Statistics

The effect of the reef restoration on fish abundance was analyzed for each group or species of fish by analyzing for the effect of BEFORE (year 2007)/AFTER (year 2012) in ANOVAs using the GLM procedure in SAS software 9.4. Copyright, SAS Institute Inc. Model residuals were tested for normal distribution by the Anderson-Darling test in the UNIVARIATE procedure in SAS. Fish were grouped into four categories "Gadidae", "Labridae", "Pleuornectiformes" and "Other" for the remaining fish species. Catch numbers were +1 log transformed prior to the statistical tests. Post-Hoc comparisons were performed with Tukey's Studentized Range (HSD) test.

Species diversity was calculated using Shannon's H index

$$H = \sum pi * \ln pi$$

and Shannon's equitability index E

$$E_H = H/\ln S$$

where p_i is the proportion of species i to the total number of all species and S is the total number of species.

Changes in abundance of cod of different size classes (<20 cm, 20 - 30 cm, >30 cm) in the area around Læsø Trindel in the BEFORE/AFTER period were examined by an ANOVA on the negative binomial distributed CPUE data from the DTU Aqua research trawl surveys by the procedure COUNTREG in SAS. A similar analysis was conducted for changes in abundance of cod caught in the gillnets in the three reef sampling areas. Test statistics for the residual test are not shown unless the test was statistically significant. A significance level (p) of 0.05 was applied to all tests.

3. Results

The total number of species caught in 2007 in the combined catches of both gear types was 33 while a total of 30 species was caught in 2012. The number of species caught in the gillnets was 27 and was similar BEFORE and AFTER the restoration, whereas the number of species caught in the fyke nets was lower following restoration: 25 BEFORE decreasing to 21 AFTER (**Table 1**). Before the restoration, goldsinny wrasse *Ctenolabrus rupestris*, corkwing *Symphodus melops*, and small-mouthed wrasse *Centrolabrus exoletus*, comprised 78% of the gillnet catches and ballan wrasse *Labrus bergylta*, corkwing and sole *Solea solea*, 64% of the fyke net catches. After the restoration, the wrasses still dominated the catches but constituted 68% of the total catch. In the fyke nets, the Labridae were no longer dominant in 2012 and the catch was more evenly distributed among the groups. Thus, both Shannon's diversity index and equitability index tended to be slightly higher after the restoration, re- flecting the more even distribution of the individual species in the community AFTER the restoration than BEFORE.

The gadoids caught in the gillnets constituted mainly of cod, saithe and some whiting and Pollack *Pollachius pollachius* (**Table 2**). Abundance of gadoids was generally low in all parts of the reef BEFORE the restoration but increased significantly AFTER for all areas (**Figure 2(a)**) (ANOVA, $p < 0.001$). Abundance increased particularly in the central part of the restored reef at 2 - 6 m depth. Here, abundance was significantly higher (Tukey, $p < 0.05$) than over the western and eastern deeper (6 - 10 m) parts of the reef. The eastern and western parts of the reef were not significantly different from each other with respect to abundance neither BEFORE nor AFTER (Tukey, $p > 0.05$).

Table 1. Number of species caught in gillnets and fyke nets in 2007 and 2012. For each year and gear the frequency of catches of the different groups of fish species relative to total catch, Shannon's diversity index H and equitability index E_H calculated using catch per unit effort.

	Gillnets		Fyke nets	
	2007	2012	2007	2012
n species	27.00	27.00	25.00	21.00
Freq. Gadidae	0.02	0.13	0.001	0.20
Freq. Labridae	0.87	0.68	0.654	0.25
Freq. Pleuornectiformes	0.06	0.09	0.235	0.30
Freq. Other	0.05	0.10	0.110	0.26
H	1.81	1.96	2.09	2.48
E_H	0.55	0.59	0.65	0.82

Table 2. Catch per unit effort for each fish species caught in gillnetsand fyke nets.

		Gillnets		Fyke nets	
Latin name	English name	2007	2012	2007	2012
Gadidae					
Gadus morhua	Cod	4.50	13.40	0.22	11.00
Pollachius virens	Saithe	0.40	3.52	0.00	0.67
Pollachius pollachius	Pollack	0.40	0.76	0.00	0.00
Merlangius merlangus	Whiting	0.30	0.04	0.00	0.00
Labridae					
Labrus bergylta	Ballan wrasse	19.80	2.32	20.11	0.00
Labrus bimaculatus	Cuckoo wrasse	4.50	0.16	0.11	0.00
Ctenolabrus rupestris	Goldsinny wrasse	29.50	59.80	8.11	8.44
Symphodus melops	Corkwing	81.00	23.24	61.89	6.33
Centrolabrus exoletus	Small-mouthed wrasse	98.70	7.04	15.33	0.11
Pleuronectiformes					
Limanda limanda	Common dab	9.60	6.52	11.22	6.22
Psetta maxima	Turbot	1.30	0.04	0.11	0.00
Pleuronectes platessa	Plaice	0.90	3.24	1.56	0.89
Microstomus kitt	Lemon sole	0.50	0.44	2.89	3.78
Platichthys flesus	Flounder	0.00	0.04	0.11	0.00
Scophthalmus rhombus	Brill	0.80	0.24	0.89	0.33
Lepidorhombus whiffiagonis	Megrim	0.00	0.00	0.11	0.00
Solea solea	Sole	3.20	1.28	21.00	6.33
Arnoglossus laterna	Scaldfish	0.00	0.04	0.00	0.00
Zeugopterus punctatus	Topknot	0.10	0.00	0.00	0.11
Other					
Icelus bicornis	Twohorn sculpin	2.30	0.00	1.00	0.00
Trachinus draco	Greater weever fish	4.30	3.40	0.22	0.22
Callionymus lyra	Common dragonet	1.50	3.80	0.78	1.78
Ciliata mustella	Five-bearded rockling	0.00	0.04	0.00	0.00
Enchelyopus cimbrius	Four-bearded rockling	0.00	0.00	1.56	1.56
Belone belone	Garfish	0.00	0.12	0.00	0.11
Entelurus aequoreus	Snake pipefish	0.00	0.00	0.33	0.00
Cyclopterus lumpus	Lumpfish	0.10	0.00	0.00	0.00
Clupea harengus	Herring	0.90	0.00	0.00	0.00
Spinachia spinachia	Ten-spined stickleback	0.10	0.60	1.11	0.11
Pholis gunnellus	Butter fish	0.10	0.36	0.56	0.44
Hyperoplus lanceolatus	Greater sandeel	0.10	0.00	0.00	0.00
Myoxocephalus scorpius	Sculpin	2.80	3.16	3.00	2.89
Taurulus bubalis	Sea scorpion	0.00	1.60	0.67	2.56
Anguilla anguilla	Eel	0.00	0.00	4.78	1.44
Zoarces viviparus	Eelpout	0.90	0.08	3.67	4.11

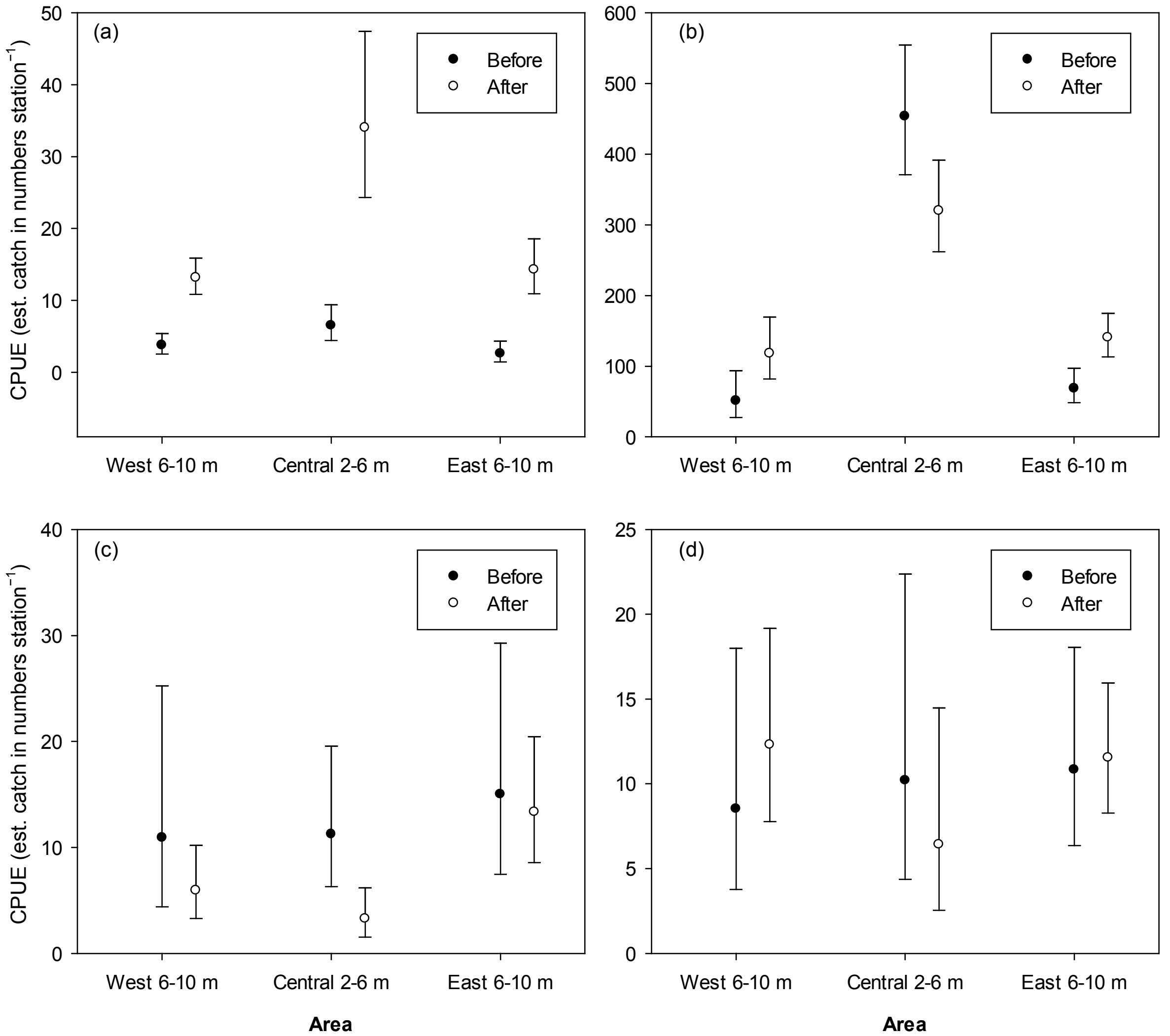


Figure 2. Catch per unit effort (CPUE) of fish caught with multi-meshed gillnets on Læsø Trindel. Estimated numbers + SE. BEFORE = 2007, AFTER = 2012. (a) Gadidae; (b) Labridae; (c) Pleuronectiformes; (d) Other.

Five species of Labridae were caught in gillnets in this study (**Table 2**). The highest abundances of these species were observed in the central shallow (2 - 6 m) part of the reef both BEFORE and AFTER the restoration (**Figure 2(b)**). However, in the BEFORE situation, the difference between the areas was more pronounced, with significantly higher abundance in the central shallow (2 - 6 m) compared to the two deeper areas (Tukey, $p > 0.005$). The abundance of Labridae in the central shallow part of the reef decreased after the restoration, although the change was not significant (ANOVA, $p = 0.0585$). In the deeper part (6 - 10 m), the abundances of representatives from this group increased in both the deeper western part (ANOVA, $p = 0.0419$) and the eastern part ($p = 0.0058$). While goldsinny wrasse increased in abundance AFTER the reef restoration, the other four species of Labridae decreased in abundance following restoration of the reef (**Table 2**).

Nine species of flatfish (Pleuronectiformes) were caught in the reef area with gillnets, most commonly dab *Limanda limanda*, and sole (**Table 2**). Abundance of these species decreased slightly after the restoration of the reef. The changes were not significantly different in the deeper western and eastern parts of the reef, but were significantly lower in the central shallow part ($p = 0.0344$) (**Figure 2(c)**). In contrast to all the other flatfish species, plaice *Pleuronectes platessa* tended to increase in abundance after the reef restoration (**Table 2**).

The remaining fish species caught in gillnets were pooled into a group called "Other" (see list of species in **Table 2**). There were no differences in abundance of this "Other" group in any of the three areas of the reef from before and after the restoration (**Figure 2(d)**).

Cod in fyke nets was the most frequently caught species (**Table 2**). The abundance of cod increased from 2007 to 2012 in all areas over the reef, although most notably in the shallow central part of the reef (West 6 - 10 m: $p = 0.0069$; East 6 - 10 m: $p = 0.0032$; Central 2 - 6 m: $p = 0.0048$) (**Figure 3(a)**). Another gadoid species, the saithe, caught both BEFORE and AFTER the restoration was in the size range 18 - 26 cm and increased in abundance after the restoration (**Table 2**). In 2007, corkwing, ballan wrasse and small-mouthed wrasse were caught most frequently in fyke nets (**Table 2**). After the restoration, catches of all three species declined but the decline of wrasses caught in fyke nets was only significant in the eastern deeper part of the reef (East 6 - 10 m: $p = 0.0415$), while catches of goldsinny wrasse remained at the same level as BEFORE (**Figure 3(b)**). Flatfish catches tended to decline but this decline was not significant in any of the reef areas. The largest declines in catches were observed for dab and sole, which were the two most abundant flatfish in the 2007 catches (**Figure 3(c)**; **Table 2**). Fish species from the "Other" group showed slightly higher catches after the restoration over the deeper eastern and western parts of the reef and lower in the central shallow part but the changes were not significant (**Figure 3(d)**).

The analyses of the size distribution of all fish caught in gillnets over the reef showed that numbers of fish >30 cm tended to increase after the restoration (**Figure 4**). The size increase was mainly due to a higher occurrence of larger cod, which aggregated around the shallow part of the reef after the restoration (**Figure 5(a)**). The proportion of cod >30 cm increased from 0.16 to 0.24 AFTER the restoration of the reef and the difference

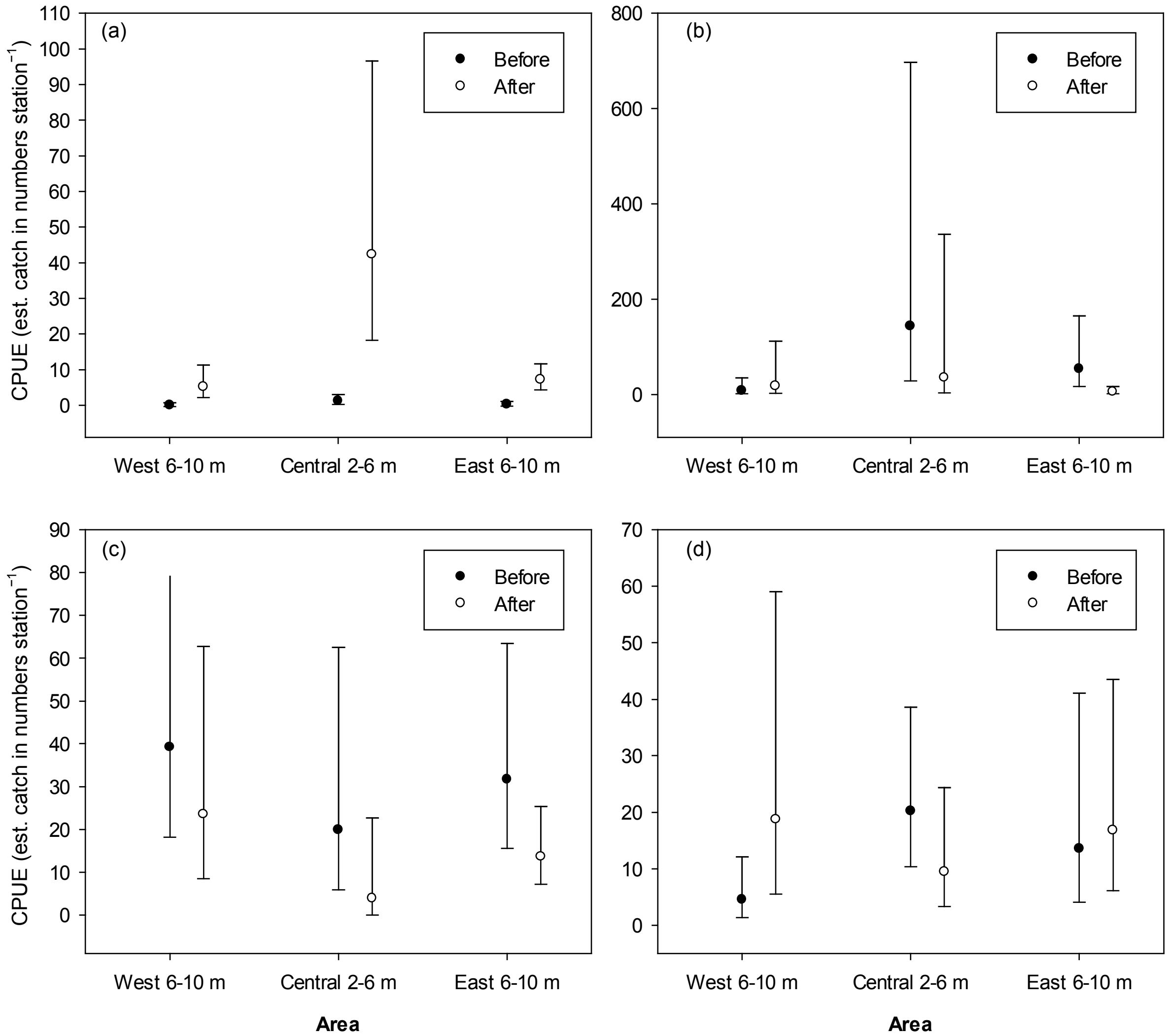


Figure 3. Catch per unit effort (CPUE) of fish caught with fykenets on Læsø Trindel. Estimated numbers + SE. BEFORE = 2007, AFTER = 2012. (a) Gadidae; (b) Labridae; (c) Pleuronectiformes; (d) Other.

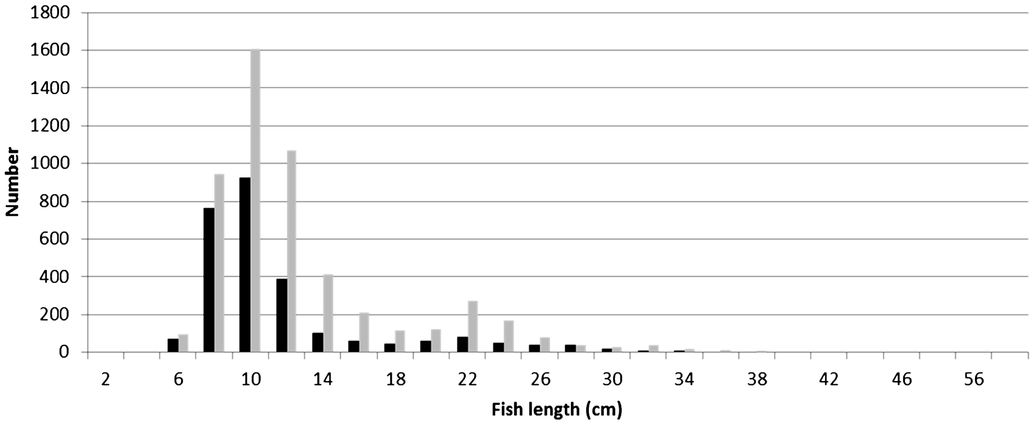


Figure 4. Length distribution of all fish caught in the multimesh gillnets BEFORE (black bars) and AFTER (light grey bars) the reef restoration.

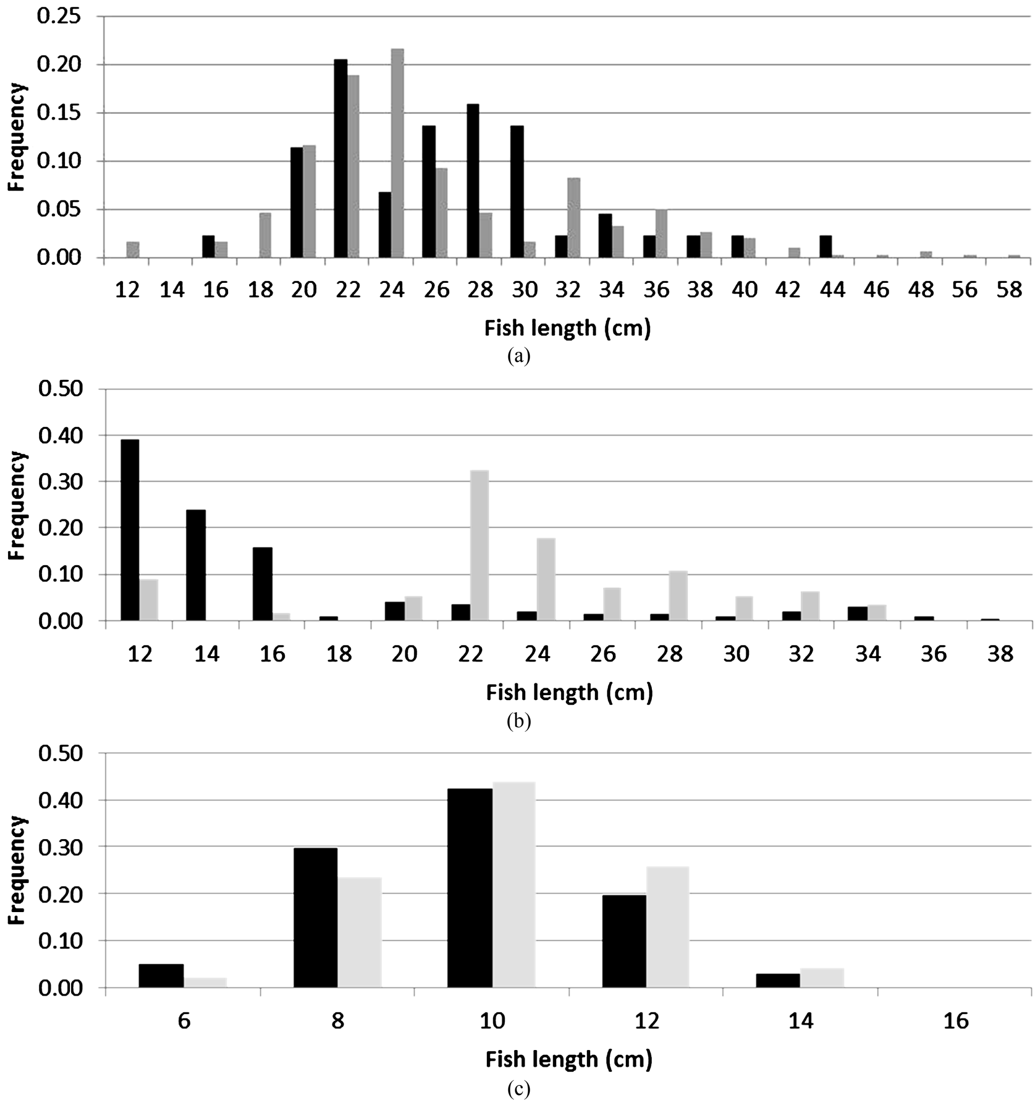


Figure 5. (a)-(c) Length frequency of cod (a), ballan wrasse (b) and goldsinny wrasse (c) caught in the multimesh gillnets BEFORE (black bars) and AFTER (light grey bars) the reef restoration.

was statistically significant (ANOVA, p = 0.0004). The abundance of juvenile cod also increased significantly after the restoration (<20 cm, ANOVA, $p < 0.0001$; 20 - 30 cm, ANOVA, p = 0.0001). Although abundance of ballan wrasse decreased after the restoration, those that were present AFTER the restoration were larger than BEFORE (**Figure 5(b)**). Goldsinny wrasse increased in abundance after the restoration with a slight shift towards larger individuals (**Figure 5(c)**).

Information from the research trawl surveys in the neighboring area showed that the abundance of cod < 20 cm did not change significantly between the BEFORE and AFTER period (ANOVA, $p > 0.55$) while cod from 20 - 30 cm (ANOVA, $p < 0.02$) and cod >30 cm (ANOVA, $p < 0.001$) significantly declined from BEFORE to AFTER (**Figure 6**). Thus, the development with respect to the abundance and population structure for cod noted over the reef following restoration did not mirror the general development in the region as a whole.

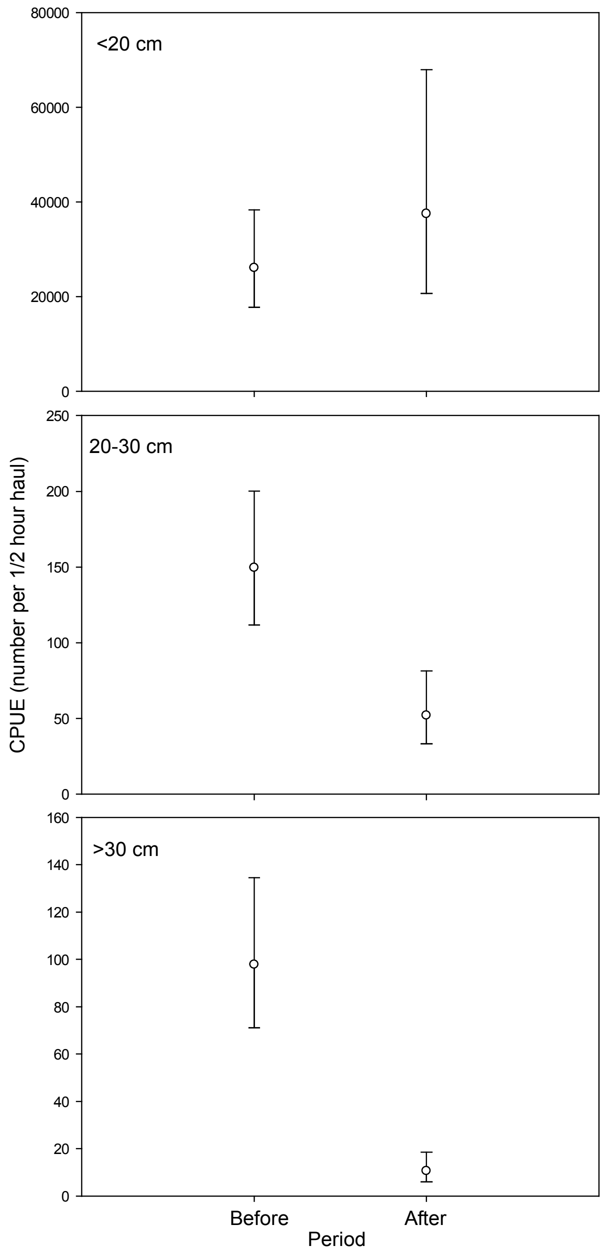


Figure 6. Catch per unit effort (CPUE) of cod in research trawl surveys within 50 km distance from Læsø Trindel. Estimated numbers + SE. BEFORE = years 2005-2007, AFTER = years 2010-2012.

4. Discussion

This study demonstrates a change in fish diversity, the distribution of species and population size characteristics for some fish species from BEFORE and AFTER reef restoration. Results from this study presented elsewhere [10] [19] documented that the reef restoration led to a re-colonization of reef regions with macroalgae. Thus, we suggest that the changes noted in the fish populations here are likely related to the restoration of the reef habitat with macroalgal vegetation.

Much of our understanding of the importance of spatial heterogeneity and structure for recruitment of reef fishes derives from studies conducted on coral reefs. However, temperate reefs differ from coral reefs in that macroalgae dominate the physical structure of temperate reefs [9]. Thus, variability in abundance and type of macroalgae between and within reefs drive the dynamics of recruitment in temperate reef fishes [2] [6]. Destruction or degradation of temperate reef habitats leading to loss of large macroalgae and dominance of opportunistic algae results in loss of spatial heterogeneity and structure that appear to be important for recruitment in reef fishes as well as other demersal species that utilise complex hard bottom habitat.

The total number of species (32) caught with the multi-meshed gillnets over the two sampling years in this study was slightly lower than the number (38) reported by [5]. These authors used multi-meshed gillnets in a rocky-bottom coastal habitat on the west coast of Sweden, north-east of the study site of this study. The fyke nets caught a further four species including the European eel *Anguilla anguilla*, bringing the total number of species caught to 36. This indicates that the combination of multi-meshed gillnets and fyke nets used in this study was sufficient to sample a wide range of the species occurring in the area. Both gears used are selective. The high size selectivity of gillnets was taken into consideration with the multi-mesh gillnets, where a broad range of mesh sizes were used to ensure a wide size range of fish. As the aim of this work was to compare the fish assemblages BEFORE and AFTER the restoration, it was assumed that the bias in species capture and size range would be similar. However, the increased complexity of the restored reef, due to both a higher variety in relief but also the presence of larger algae, may have reduced the fishing efficiency of the nets, and the catches in the 2012 surveys may thus be underestimates.

The result that more complex habitats lead to higher species diversity and abundance than less complex ones is not unexpected and has been shown earlier for tropical and temperate marine habitats [22] [23]. In this study, however, we did not alter the habitat from a smooth bottom to a complex bottom, but rather attempted to increase the complexity by restoring the larger boulders, creating more relief and providing a physically stable substrate for the development of macroalgae [10]. The (Ash-Free Dry Weight) AFDWm^{-2} of the macroalgal biomass increased by more than twofold at 5 - 6 m depth and this was especially due to an increase in the brown algae (Phaeophyta) (Karsten Dahl, upublished data). Apparently, the increased complexity of the restored reef was not sufficient to result in a significant increase in fish species richness. In the general Kattegat area, a decline in sea bottom temperature of about 0.75˚C between 2007 and 2011 was associated with a decline in species richness of 3 - 4 species per degree [24]. The decline in number of species in the fyke nets could, therefore, be due to this temperature decrease, but this does not explain the similar number of species in the gillnet catches in 2007 and 2012. The species decline in the fyke nets was driven by fewer flatfish species and the lack of ballan wrasse in the 2012 catches and may be due to a less favorable habitat for these species following reef restoration.

In this study, although species richness declined in the fyke net catches, Shannon's diversity index increased. The dominance of Labridae in the catches before the restoration decreased after the restoration resulting in a more even distribution of species especially in the fyke net catches. Abundance of the resident fish species, goldsinny wrasse tended to increase. Goldsinny wrasse is a resident species with high affinity to rocky substrate [25] [26]. Kelp forests, similar to that developed in the restored reef [10] provide ample feeding opportunities for this species [27]. Since refuge availability seems to be the main limiting factor determining the abundance of goldsinny wrasse [28], an increase in abundance of this species was expected. The larger labrid, the ballan wrasse, decreased in abundance AFTER but a higher proportion of larger fish inhabited the reef after the restoration than BEFORE. The ballan wrasse is a sedentary, territorial species with slow growth and it is a protogynous hermaphrodite [29]. The presence of larger sizes of fish is important in sex-changing fish species to maintain reproductive potential and population size [30]. Thus, the presence of larger specimens is important to secure sufficient sex ratios for effective mating. Due to the restricted home range of the species, even a small area with improved habitat and protected from fisheries would be sufficient for this and other Labridae species. The results suggest that the restored reef provided better opportunities for the larger fish predators and improved habitat for recruitment of wrasses, providing protection and potentially increasing the reproductive potential due to the increase in fish size.

The distribution of commercially important gadoids depends on the presence of heterogeneous substrate types and associated biogenic growth [31] [32]. Vegetated habitats, *i.e.* shallow rocky areas with algae and soft bottom sediment with seagrass beds, are important nursery areas for young juvenile cod [33]. In this study, the gadoids cod and saithe increased in abundance by a factor of 3 - 6 after the restoration. Primarily the larger juveniles (>30 and >20 cm in length for cod and saithe, respectively) increased in abundance. The increase in abundance of juveniles in this study was not reflected in the bottom trawl surveys for the Kattegat stock component [21] [34], which show a negative trend. Furthermore, the analysis on the bottom trawl data performed in this study showed a marked decline in the abundance of larger juvenile cod in the area surrounding the reef (within 50 km). These data were used in lieu of a lack of reference site for sampling before and after restoration and provide an opportunity to compare the development in abundances of different sizes of cod in the period before and after the reef restoration.

Notably, the shallow part of the reef (2 - 6 m) attracted the highest abundance of cod AFTER the restoration. This is in line with the observations of [5], where the highest abundance of fish was found in shallow water (0 - 3 m and 3 - 6 m) kelp habitats and significantly lower abundance in the deeper (6 - 10 m) rocky habitat. The study of [5] was conducted in the Swedish archipelago north-east of the site of the reef restoration in this study. Juvenile cod are especially susceptible to limitations in demersal habitat due to their density-dependent mortality [35], suggesting a high vulnerability to the loss of complex habitats and the need to preserve these habitats for maintaining or rebuilding severely depleted stocks [36].

Fish densities are positively related to vegetation biomass [9] and the increased macroalgal biomass [10] was expected to increase fish densities in the restored area of the reef. The macroalgal dominance in temperate reefs may lead to high variability in fish assemblages and broader use of a reef habitat due to linkages between habitat attributes and life-stage strategies or behavioral responses in reef associated fishes [6]. Kelp forests, such as the one in the process of forming on the restored reef area [10], are known to be important feeding grounds for many fish species including cod [27].

Habitat degradation with loss of forest-forming macroalgae can be compared to kelp-harvest activity, except in the former case this impact is of a more permanent nature because before the reef stability or structure has been restored, macroalgae cannot re-establish. In newly-harvested kelp areas in Norway, the number of juvenile gadoids was 92% lower than in un-harvested areas [32]. Lower abundances of gadoids persisted one year after the harvest. This is not unexpected considering gadoids utilize kelp forests as feeding and nursery areas and for shelter from larger predators [27]. Cod seek refuge in macroalgae to avoid predation in the presence of actively foraging predators [31], so juvenile cod tend to be segregated from larger cod [37]. In this study, the restoration of the reef resulted in higher abundances of juvenile cod (<20 cm) as well as a higher proportion of larger (>30 cm) cod in the catches. The increased complexity of the restored reef habitat may, thus, have provided shelter and food for the smaller cod and better predation opportunities for the larger cod.

The increased proportion of larger cod, increased abundance of saithe, and increased proportion of larger specimens of the larger labrid, the ballan wrasse, in the restored reef area may reflect greater prey availability on the restored reef. The increased frequency of larger cod in the catches on the restored reef was in contrast to the decline of larger cod in the catches from the bottom trawl surveys in the area surrounding the restored reef. The generally higher frequencies of larger cod in our catches further reflect the affinity of larger cod to rocky substrate. The Kattegat cod stock is a unique population the Kattegat and has, since 2000, been considered outside safe biological limits by ICES [21]. Commercial fishing continues to take place and, accordingly, the reduction in reproductive capacity of this stock is considered to be due to reduced stock size rather than habitat loss [38]. The fishery in the area is dominated by trawls [21]; thus the restored reef where trawling is virtually impossible, could act as a refuge from fishing for the larger cod and contribute to the reproductive performance of the local population and, ultimately, recruitment.

Restoration is a rapidly developing field of research requiring clear objectives, appropriate definition of success criteria, and development of effective methodology to measure the success [39]. Most assessments focus on ecological attributes and although socio-economic attributes also should be targeted, it is important to measure the success of restoration to further this research field [39]. The restoration of the temperate reef in this study focused on ecological attributes; the results on the physical and social attributes will be addressed elsewhere. In this study we showed that the reef restoration brought about changes in the fish community. Dominance of wrasses was maintained after the restoration, but was less obvious than BEFORE the restoration due to the increased abundance of several other species resulting in a more even distribution of species. This suggests a higher variety of refuge and suitable micro-habitat types AFTER the restoration than BEFORE. Commercially important gadoid species, cod and saithe, increased 3 - 6-fold in abundance after the restoration. The restored shallow part of the reef seemed to particularly attract cod and goldsinny wrasse, although not significantly for the latter species. A higher proportion or larger specimens of cod and ballan wrasse after the restoration indicated improved foraging opportunity for the larger fish and an increase in the reproductive potential for these species. The concurrent increase in abundance of smaller cod (<20 cm) and higher proportion of larger cod (>30 cm) indicated also an increase in refuge availability.

Acknowledgements

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References

[1] Graham, M.H. (2004) Effects of Local Deforestation on the Diversity and Structure of Southern California Giant Kelp Forest Food Webs. *Ecosystems*, **7**, 341-357. http://dx.doi.org/10.1007/s10021-003-0245-6

[2] Christie, H., Jørgensen, N.M. and Norderhaug, K.M. (2007) Bushy or Smooth, High or Low; Importance of Habitat Architecture and Vertical Position for Distribution of Fauna on Kelp. *Journal of Sea Research*, **58**, 198-208. http://dx.doi.org/10.1016/j.seares.2007.03.006

[3] Hunter, W.R. and Sayer, M.D.J. (2009) The Comparative Effects of Habitat Complexity on Faunal Assemblages of Northern Temperate Artificial and Natural Reefs. *ICES Journal of Marine Science*, **66**, 691-698. http://dx.doi.org/10.1093/icesjms/fsp058

[4] ICES (2007) Report of the International Bottom Trawl Survey Working Group (IBTSWG). ICES CM 2007/RMC, 05:195 pp.

[5] Stål, J., Pihl, L. and Wennhage, H. (2007) Food Utilization by Coastal Fish Assemblages in Rocky and Soft Bottoms on the Swedish West Coast: Inference for Identification of Essential Fish Habitats. *Estuarine*, *Coastal and Shelf Science*, **71**, 593-607. http://dx.doi.org/10.1016/j.ecss.2006.09.008

[6] Pérez-Matus, A. and Shima, J.S. (2010) Disentangling the Effects of Macroalgae on the Abundance of Temperate Reef Fishes. *Journal of Experimental Marine Biology and Ecology*, **388**, 1-10. http://dx.doi.org/10.1016/j.jembe.2010.03.013

[7] Wieland, K., Pedersen, E.M.F., Olesen, H.J. and Beyer, J.E. (2009) Effect of Bottom Type on Catch Rates of North Sea Cod (*Gadus morhua*) in Surveys with Commercial Fishing Vessels. *Fisheries Research*, **96**, 244-251. http://dx.doi.org/10.1016/j.fishres.2008.11.010

[8] Dahl, K., Lundsteen, S. and Helmig, S. (2003) Stenrev, Havbundens Oaser. Gads Forlag, Copenhagen, Denmark. (In Danish)

[9] Carr, M.H. (1994) Effects of Macroalgal Dynamics on Recruitment of a Temperate Reef Fish. *Ecology*, **75**, 1320-1333. http://dx.doi.org/10.2307/1937457

[10] Stenberg, C., Støttrup, J.G., Dahl, K., Lundsteen, S., Göke, C. and Andersen, O.N. (2013) Ecological Benefits from Restoring a Marine Cavernous Boulder Reef in Kattegat, Denmark. Final Report to the European Commission Regarding LIFE06 NAT/DK000159 Blue Reef, 47.

[11] Dahl, K., Stenberg, C., Lundsteen, S., Støttrup, J., Dolmer, P. and Tendal, O.S. (2009) Ecology of Læsø Trindel—A Reef Impacted by Extraction of Boulders. National Environmental Research Institute, Technical Report No. 757.

[12] Almada, V.C., Henriques, M. and Gonçalves, E.J. (1999) Ecology and Behaviour of Reef Fishes in the Temperate North-Eastern Atlantic and Adjacent Waters. In: Almada, V.C., Oliveira, R.F. and Gonçalves, E.J., Eds., *Behaviour and Conservation of Littoral Fishes*, ISPA, Lisbon, 33-68.

[13] Wennhage, H. and Pihl, L. (2002) Fish Feeding Guilds in Shallow Rocky and Soft Bottom Areas on the Swedish West Coast. *Journal of Fish Biology*, **61**, 207-228. http://dx.doi.org/10.1111/j.1095-8649.2002.tb01772.x

[14] Swales, S. (1994) Habitat Restoration Methods—A Synthesis. In: Cowx, I.G., Ed., *Rehabilitation of Freshwater Fisheries*, Fishing News Books, Oxford, 133-137.

[15] Rinkevich, B. (2014) Rebuilding Coral Reefs: Does Active Reef Restoration Lead to Sustainable Reefs? *Current Opinion in Environmental Sustainability*, **7**, 28-36. http://dx.doi.org/10.1016/j.cosust.2013.11.018

[16] Chapman, M.G. (1999) Improving Sampling Designs for Measuring Restoration in Aquatic Habitats. *Journal of Aquatic Ecosystem Stress and Recovery*, **6**, 235-251. http://dx.doi.org/10.1023/A:1009987403481

[17] Barbier, E. (2006) Natural Barriers to Natural Disasters: Replanting Mangroves after the Tsunami. *Frontiers in Ecology and the Environment*, **4**, 124-131. http://dx.doi.org/10.1890/1540-9295(2006)004[0124:NBTNDR]2.0.CO;2

[18] Kennedy, V.S., Breitburg, D.L., Christman, M.C., Luckenbach, M.W., Paynter, K., Kramer, J., Sellner, K.G., Dew-Baxter, J., Keller, C. and Mann, R. (2011) Lessons Learned from Efforts to Restore Oyster Populations in Maryland and Virginia, 1990 to 2007. *Journal of Shellfish Research*, **30**, 719-731. http://dx.doi.org/10.2983/035.030.0312

[19] Anonymous (2013) Post Bathymetry and Stability of Reef Structures. Technical Final Report LIFE06 NAT/DK/000159-Blue Reef, Annex 15, 5.
http://naturstyrelsen.dk/naturbeskyttelse/naturprojekter/blue-reef/undersoegelser-investigations/

[20] Eigaard, O.R., Støttrup, J.G. and Hovgård, H. (2000) Udvikling af standard garnserie til brug ved rutinemæssig bestandsanalyse af flad-og rundfisk i marine lavvandede områder. DFU-Report nr. 78-00. (In Danish)

[21] ICES (2012) Report of the Baltic Fisheries Assessment Working Group 2012 (WGBFAS). ICES CM. 2012/ACOM: 10, 12-19 April 2012, ICES Headquarters, Copenhagen, 859 p.

[22] Jones, G.P. (1988) Ecology of Rocky Reef Fish of North-Eastern New Zealand: A Review. *New Zealand Journal of Marine and Freshwater Research*, **22**, 445-462. http://dx.doi.org/10.1080/00288330.1988.9516315

[23] Gratwicke, B. and Speight, M.R. (2005) The Relationship between Fish Species Richness, Abundance and Habitat Complexity in a Range of Shallow Tropical Marine Habitats. *Journal of Fish Biology*, **66**, 650-667.
http://dx.doi.org/10.1111/j.0022-1112.2005.00629.x

[24] Bryndum, K.M. (2013) Fish Species Composition in the Inner Danish Waters. An Analysis of the Fish Assemblage in Light of Changes in Sea Temperature. Master's Thesis, Center for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen.

[25] Sayer, M.D.J., Gibson, R.N. and Atkinson, R.J.A. (1993) Distribution and Density of Populations of Goldsinny Wrasse (*Ctenolabrus rupestris*) on the West Coast of Scotland. *Journal of Fish Biology*, **43**, 157-167.
http://dx.doi.org/10.1111/j.1095-8649.1993.tb01185.x

[26] Gjøsæter, J. (2002) Distribution and Density of Goldsinny Wrasse (*Ctenolabrus rupestris*) (Labridae) in the Risør and Arendal Areas along the Norwegian Skagerrak Coast. *Sarsia*, **87**, 75-82.
http://dx.doi.org/10.1080/003648202753631758

[27] Norderhaug, K.M., Christie, H., Fosså, J.H. and Fredriksen, S. (2005) Fish-Macrofauna Interactions in a Kelp (*Laminaria hyperborea*) Forest. *Journal of the Marine Biological Association of the United Kingdom*, **85**, 1279-1286.
http://dx.doi.org/10.1017/S0025315405012439

[28] Costello, M.J. (1991) Review of the Biology of Wrasse (Labridae: Pisces) in Northern Europe. *Progress in Underwater Science*, **16**, 29-51.

[29] Villegas-Ríos, D., Alos, J. and March, D. (2013) Home Range and Diel Behavior of the Ballan Wrasse, *Labrus bergylta*, Determined by Acoustic Telemetry. *Journal of Sea Research*, **80**, 61-71.
http://dx.doi.org/10.1016/j.seares.2013.02.009

[30] Alonzo, S.H. and Mangel, M. (2004) The Effects of Size-Selective Fisheries on the Stock Dynamics of and Sperm Limitation in Sex-Changing Fish. *Fisheries Bulletin*, **102**, 1-13.

[31] Gotceitas, V., Fraser, S. and Brown, J.A. (1995) Habitat Use by Juvenile Atlantic Cod (*Gadus morhua*) in the Presence of an Actively Foraging and Nonforaging Predator. *Marine Biology*, **123**, 421-430.
http://dx.doi.org/10.1007/BF00349220

[32] Lorentsen, S.H., Sjøtun, K. and Grémillet, D. (2010) Multi-Trophic Consequences of Kelp Harvest. *Biological Conservation*, **143**, 2054-2062. http://dx.doi.org/10.1016/j.biocon.2010.05.013

[33] Stål, J., Paulsen, S., Pihl, L., Rönnbäck, P., Söderqvist, T. and Wennhage, H. (2008) Coastal Habitat Support to Fish and Fisheries in Sweden: Integrating Ecosystem Functions into Fisheries Management. *Ocean & Coastal Management*, **51**, 594-600. http://dx.doi.org/10.1016/j.ocecoaman.2008.06.006

[34] Vinther, M. and Eero, M. (2013) Quantifying Relative Fishing Impact on Fish Populations Based on Spatio-Temporal Overlap of Fishing Effort and Stock Density. *ICES Journal of Marine Science*, **70**, 618-627.
http://dx.doi.org/10.1093/icesjms/fst001

[35] Meyers, R.A. and Cadigan, N.G. (1993) Density-Dependent Juvenile Mortality in Marine Demersal Fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 1576-1590. http://dx.doi.org/10.1139/f93-179

[36] Gregory, R.S. and Anderson, J.T. (1997) Substrate Selection and Use of Protective Cover by Juvenile Atlantic Cod

Gadus morhua in Inshore Waters of Newfoundland. *Marine Ecology Progress Series*, **146**, 9-20. http://dx.doi.org/10.3354/meps146009

[37] Fraser, S., Gotceitas, V. and Brown, J.A. (1995) Interactions between Age-Classes of Atlantic Cod and Their Distribution among Bottom Substrates. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 305-314. http://dx.doi.org/10.1139/f95-183

[38] Svedäng, H., Stål, J., Sterner, T. and Cardinale, M. (2010) Subpopulation Structure in Cod (*Gadus morhua*) Puts Strain on the Management Toolbox. *Reviews in Fisheries Science*, **18**, 139-150. http://dx.doi.org/10.1080/10641260903511420

[39] Wortley, L., Hero, J.M. and Howes, M. (2013) Evaluating Ecological Restoration Success: A Review of the Literature. *Restoration Ecology*, **21**, 537-543. http://dx.doi.org/10.1111/rec.12028

Paper III

Ecological effects of boulder reef restoration on prey abundance and feeding behaviour of fish

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Manuscript

ECOLOGICAL EFFECTS OF BOULDER REEF RESTORATION ON PREY ABUNDANCE AND FEEDING BEHAVIOUR OF FISH

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ABSTRACT

The aim of this study was to estimate the effect of a boulder reef restoration on the abundance of potential fish prey on the reef. We examined benthos, epifauna and fish stomachs to assess the type and magnitude of prey consumed by fish caught in and around the reef. The ash free dry weight of cod (*Gadus morhua*) stomach content increased threefold after restoration and was dominated by the invertebrates Galatheidae, Brachyura, and fish. The invertebrate prey items had increased fivefold in abundance and 14-fold in biomass after restoration. The increased prey abundance was most evident for species associated with vegetation and hard bottom habitats. Diet of juvenile saithe (*Pollachius virens*) was predominantly invertebrates and switched to piscivorous at around 20 cm in length. Saithe had a moderate (39%) diet overlap with cod. Saithe fed predominantly on pelagic species whereas demersal species were consumed by cod. Goldsinny wrasse (*Ctenolabrus rupestris*) and corkwing wrasse (*Symphodus melops*) had a large feeding niche overlap (80%) and fed mainly on benthic species with high affinity to hard bottom habitats.

KEY WORDS: boulder reef, habitat restoration, benthic fauna, stomach content, feeding ecology, *Gadus morhua, Pollachius virens, Labrus sp.*

INTRODUCTION

Boulder reefs have tremendous biodiversity and production both in tropical and temperate areas. The biodiversity, abundance and biomass of substrate associated prey have been shown to be approximately three times higher on temperate hard bottom habitats compared to the surrounding sandy habitats (Stål et al. 2007). This is largely due to the macroalgae that settle on the large stable substrate provided by the boulders. One kelp algae can hold up to 90,000 individuals and in some areas the average fauna density exceeds half a million animals pr. m^2 (Christie et al. 2009). Vegetation thus provides good feeding opportunities for several fish species such as juvenile cod (Wennhage & Pihl 2002, Norderhaug et al. 2005). After harvesting a kelp forest the abundance of juvenile cod dropped by 92% (Lorentsen et al. 2010) demonstrating the importance of this habitat. However, at the population level, the quantitative importance of temperate boulder reefs still needs further investigation.

Marine aggregate extraction of boulders and dredging fishery on reefs reduce the complexity of the sea bed (Dahl et al. 2003). The complexity is further reduced by the removal or destruction of associated biogenic structures (Carr 1994). Boulder extraction in Denmark is believed to have destroyed many coastal boulder reefs with a presumed high loss of biomass and numbers of hard bottom species (Dahl et al. 2003). Due to limited availability of boulder and rocks in Danish territory this resource was heavily extracted from the coastal waters to construct piers, jetties and other coastal constructions peaking in the 1950s and 1960s (Dahl et al. 2003). It is still unknown where and how many reefs were destroyed by this activity, which went on for at least a century.

According to historical maps the water depth of the Danish boulder reef Læsø Trindel was ~1.25 m in 1831 and 1911. Extraction of boulders from the reef for the construction industry increased the depth to approximately 4 m by the 1970s. In 1991, Læsø Trindel was included in the National Marine Monitoring Program and became part of the NATURA 2000. The monitoring program soon revealed that the conservation in the area was not satisfactory (Fredshavn et al. 2014). The extraction of boulders had destabilized the reef, and smaller stones with attached macroalgae grated against the other stones, scraping off most of the attached flora and fauna. In some cases, the attached macroalgae functioned as a “sail” during periods of high physical stress, dragging the stones with vegetation into the deeper areas leaving the algae to decompose and creating hypoxic bottom conditions. Reef habitats are included in the EU Habitats Directive and 51 areas have been included in the Danish NATURA 2000 network. Denmark is thus obliged to protect and restore these important habitats. However, to our knowledge, no boulder reef restoration in marine areas has previously been attempted and, thus, there are no guidelines available to ensure a responsible approach.

The condition of Læsø Trindel is representative of the condition of the majority of shallow boulder reefs in Denmark. Thus the outcome of this project is especially important for the management of reefs in Danish waters where this habitat type is less common. The results are, however, also useful for the management of temperate reefs in other regions as the method applied in this project is readily copied and the loss of habitats is a global problem. Especially biogenic and coral reefs have been damaged (Watling & Norse 1998, Airoldi & Beck 2007, Rossi 2013) but only few studies have investigated the destructive effect of fishery on boulders (Freese et al. 1999, Gordon 2002, Gage et al. 2005).

The main purpose of this project was to restore and protect the rich biota inhabiting temperate boulder reefs. This was done through stabilization of the remaining reef. In this study, we investigated the effect of the restoration on the abundance of prey for fish and examined fish stomachs to assess the type and mass of prey consumed by fish caught in and around the reef. In addition, feeding behaviour of four key fish species was investigated with special focus on the breadth of the feeding niches and dietary overlap. The overall effect of the restoration on the abundance and biodiversity of fish is discussed in Støttrup et al. (2014).

MATERIALS & METHODS

Study area and restoration of the reef

The field study was conducted on the boulder reef Læsø Trindel located 12 km north-east of the Island of Læsø in Kattegat (Stenberg et al. 2015) (**Fig. 1**). Approximately 27,400 m^2 of seabed was covered by 100,000 tons of boulders deposited at three predefined areas at Læsø Trindel from June to September in 2008. The boulders stabilized the existing reef, reintroduced the cave forming reef structures and shallower parts of the reef.

Effect analysis

The effect of the restoration of Læsø Trindel was monitored by a before-after approach. The baseline study, before restoration¸ was conducted in 2007, while the after study was conducted in 2012. The effect analysis sought to clarify the effect of the reef restoration on fishes, benthic fauna and vegetation. However, only the effect of reef restoration on fish feeding behaviour is described here.

Benthic fauna

Available prey was quantified *before* restoration of the reef in the early summer 2007 and after restoration in the early summer 2012. In 2007 sampling was carried out at 5 and 10 m depths. In 2012 sampling was done at the same depths but also at the reintroduced shallower part of the reef at 3 m depth. Sampling was carried out with help of a metal frame (1/6 m^2) that was dropped randomly on the seabed from the boat. A diver operating a suction sampler with a 1 mm filter system collected both sessile and mobile hard bottom fauna from the upper 10 cm of the seabed within the metal frame. In cases where stones were too large for the suction sampler (≥10 cm), the stones were picked by hand and added to the filter box. When the stones were too large for handpicking, the biota was detached with a putty knife during suction. All samples were immediately preserved in 4% formaldehyde buffered with borax.

The sampling method was the same in 2007 and 2012 except for the addition of 3 m depth. Furthermore, as the restored reef area in 2012 mostly consisted of larger boulders, the metal frame was substituted with a slightly flexible frame of 0.1 m^2. Samples could thereby be taken on top of the boulders as well as on the sides.

In the laboratory, fauna was identified to the lowest possible taxonomical group and quantified. All fauna organisms (sessile or not) were organized according to habitat use and labeled either *pelagic*, *sediment*, *vegetation* or *hard bottom habitat* based on the descriptions by Hayward and Ryland (1995), Kirkegaard (1992), Mortensen (1924) and Tebble (1966). These habitat labels were used by Wennhage & Pihl (2002) to demonstrate the different feeding modes of the same fish species in different habitats. Prey that could only be identified to taxonomical class or above was not assigned to any habitat type.

Fish stomachs

Sampling of cod (*Gadus morhua*), saithe (*Pollachius virens*), goldsinny wrasse (*Ctenolabrus rupestris*) and corkwing wrasse (*Symphodus melops*) for feeding analysis was planned to be conducted just after the benthic fauna investigation in 2007, but a long period with bad weather conditions and logistic problems postponed the investigation to October 2007. In 2012 investigations was conducted in June and again in October. The fish were caught using multi-meshed gillnets at the same sampling sites as for the benthic fauna. The nets were deployed just before sunset and retrieved approximately 2 hours later. To frighten inactive fish into the nets an iron chain was towed around the nets just before retrieval. To prevent decomposition of stomach content, the gillnets with the fish catch were immediately placed on ice after retrieval and frozen to -18 °C within 2-4 hours after retrieval of the nets.

In the laboratory the fish were defrosted, length measured and wet weighed. In cod the gut was defined as the digestive tract to the pylorus sacs, while for goldsinny wrasse it defined the entire digestive tract. The gut was removed and conserved in 70% ethanol. Gut content was analysed under binocular microscope and dietary items were identified to the lowest possible taxonomical group. The level of decomposition of the prey items was assessed on a scale from one to three, where one was no signs of digestion and three was almost digested. The weight of prey items on decomposition level one and two was based on calculations of volume assuming a cylindrical shape of the prey items. Prey items were grouped according to the taxonomical phylum and classes. Crustacean Malacostraca was furthermore subdivided into their taxonomical order, suborder or family. All prey organisms were organized according to habitat use as either *pelagic*, *sediment*, *vegetation* or *hard bottom habitat* in the same way as the benthic samples.

Statistical analysis

Benthic fauna

Statistical analysis of prey abundance and biomass pr. m^2 before and after restoration proved difficult as the area sampled changed from being two-dimensional to three-dimensional. Data is thus presented here as average pr. m^2 seabed for 5-6 m 9-10 m depth before restoration and 3, 5-6 m and 9-10 m depth after restoration. The same was the case for prey in cod stomachs organized according to habitat use.

Fish stomachs

The effect of reef restoration and fish length on species composition of prey in the stomach content of cod tested in a GLM model (equation 1) that was stepwise reduced. Weight data was expressed in mg and converted to ln+1 before statistical analysis. Prey species found in cod stomachs in June and October 2012 was tested for effect of season. If no effect of season was found in June and October 2012, data were pooled and tested together against October 2007. If an effect of season was found between June and October 2012 data, only stomach content from October 2007 and October 2012 were compared in further analysis. The following variables were used: year (2007 and 2012), prey species (caught in both 2007 and 2012).

$$(\log(Prey_{weight} + 1)) = Period + Fish\ length + Period * fish\ length \qquad \text{(equation 1)}$$

Where $Prey_{weight}$ is prey weight in mg, *Period* is before or after restoration of the reef and *Fish length* is the total length of the investigated fish, *Period * Fish length* represents the interaction effect between *Period* and *Fish length*.

The same method was applied for analysis of prey organized according to habitat use. Here *Period* was exchanged with *Habitat*. Residuals from GLMs where checked for normality and if not normally distributed we also performed a Wilcoxon statistical test.

Diet overlap

The degree of interspecific diet overlap was assessed using the Schoener overlap index (Schoener 1968):

$$D = 1 - ½ \sum |p_{ij} - p_{ik}| \qquad \text{(equation 2)}$$

where D is the percentage overlap between species j and species k. p_{ij} and p_{ik} *are* the proportion resource i is of the total resources used by species j and k. The index ranges from 0.0 for entirely dissimilar diets to 1.0 when the compositions of the predator diets are identical. Langton (1982) introduced three categories of diet overlap as low (D=0-0.29), moderate (D=0.3-0.59) or high (D≥0.6).

RESULTS

Before restoration of the reef a total of 69 cod and 69 goldsinny wrasse were caught for stomach analysis in October 2007 (**Table 1**). Of these 1 cod and 8 goldsinny wrasses had empty stomachs. After restoration in June 2012 a total of 68 cod, 12 goldsinny wrasse and 13 corkwing wrasse were caught for stomach analysis. In October 2012 after restoration 38 cod and 88 saithe were caught where 1 cod and 14 saithe had empty stomachs.

Benthic fauna

The average abundance of benthic fauna caught on the reef using the suction sampler increased five times after restoration from an overall 6,722 to 31,534 individuals pr. m^2 (**Fig. 2a & b**). This increase was especially pronounced for crustacean which increased 19-fold from 1,095 individual to 20,797 pr. m^2. The largest increase was observed for smaller crustaceans but also larger groups increased – Brachyura increased seven-fold. Gastropods also increase from approximately 255 individuals to 5,494 pr. m^2. Fish increased from an average of 2 individuals pr. m^2 to 6. Bivalves on the other hand decreased from 4,341 to 1,653 pr. m^2. In terms of biomass, the overall increase in Ash Free Dry Weight (AFDW) was 14-fold pr. m^2.

Fish stomachs

Before reef restoration in October 2007 very few fish were found in cod stomachs and the main prey group was smaller crustaceans such as Gammaridea (**Table 3a-d**). Gammaridea and bivalves decreased significantly in cod diet from 2007 to 2012 (GLM; P<0.0001 and P=0.001). After restoration the biomass of especially the larger crustaceans such as crabs increased significantly in cod stomachs from 2007 to 2012 (see all P-values in **Table 2**). This was the case for the Pleocyemata (GLM; P<0.0001), Brachyura (GLM; P<0.0001) and Galatheidae (GLM; P<0.0001). The biomass of fish also increased in cod stomachs from 2007 to 2012 and constituted 28-87% of the biomass in larger cod (20-35 and >35 cm) stomachs with wrasses (*Labrus* sp.) and rock gunnel (*Pholis gunnellus*) being the most abundant fish species. However, the increase in fish biomass was only borderline significant (GLM; P=0.06).

For saithe a change of diet was observed for fish around 20 cm (**Table 3b**). The most important prey group for small juvenile saithe (<20 cm) regarding biomass was copepods (62%). For larger juvenile saithe (≥20 cm) fish was the most important prey group comprising 94.2% of the stomach content. The most dominant fish species in saithe stomachs was sandeel (*Ammodytidae sp.*). The Atlantic horse mackerel (*Trachurus trachurus*) was also observed in high numbers and the rest were unidentifiable adult or larval fish.

For juvenile goldsinny wrasse the most important prey group in biomass (<10 cm) before restoration was Malacostraca that comprised 73.6% dominated by Gammaridae (**Table 3c**). After, *in* June 2012 the most important prey groups had changed to bivalves and other prey items. For adult goldsinny wrasse the most important prey groups were Malacostraca but especially other prey items that comprised approximately 55% of the total biomass.

Juvenile corkwing wrasse (<15 cm) fed exclusively on polychaetes (**Table 3d**). The biomass of the diet of adult corkwing (15-20 cm) was more diverse and consisted of 57% Malacostraca, 28% other prey (polychaetes and Arachnida) and 13% gastropods.

The Schoener overlap index shows a moderate diet overlap (0.39) of cod and saithe after the restoration of the boulder reef. The overlap of goldsinny wrasse and corkwing wrasse diet was high (0.8).

Habitat

The average abundance of organisms associated with vegetation increased from approximately 1500 pr. m^2 in June 2007 to 27,000 pr. m^2 in June 2012 (**Fig. 3a**) – an increase of 18-fold. For sediment associated fauna the abundance doubled. The average biomass of fauna associated with hard bottom habitat increased 50-fold from 2 g AFDW to 106 g AFDW (**Fig. 3b**). For fauna associated with vegetation and sediment the biomass increased by 2- and 3-fold, respectively. No change was observed for the fauna associated with the pelagic area.

The increase of prey organisms could also be observed in cod diet (**Fig. 4**). The biomass of prey associated with *sediment*, *vegetation* or *hard bottom habitat* all increased significantly in cod stomachs after the restoration (GLM and Wilcoxon; $P<0.01$).

DISCUSSION

This study showed the potential of restoring a boulder reef and reintroducing rich biota providing ample prey for resident fish species. The increase in benthic fauna of five- and 14-fold in abundance and biomass, respectively, and in cod stomach content of seven- and three-fold provide evidence of the potential marine production and ecosystem benefits we would forgo if we neglect to restore impacted reefs. The encouraging increase in biomass of flora and fauna shown here suggests that restoring temperate reefs can be beneficial for the environment and the method can be applied to other marine ecosystems similar to Kattegat. To our knowledge, no other major ecological changes have occurred in the area of Læsø Trindel between 2007 and 2012 and any changes in prey availability is thus attributed the boulder reef restoration.

Before restoration the macroalgal community on Læsø Trindel was dominated by fast-growing opportunistic species which indicated an unstable reef structure (Stenberg et al. 2015). Fast-growing ephemeral species are usually associated with relatively low abundances of invertebrate fauna compared to other macroalgae species (Christie et al. 2009). The reef restoration and stabilization of the substrate on Læsø Trindel allowed the perennial algae to grow and greatly increased the overall macroalgal biomass (Stenberg et al. 2015). Macrophytes have been shown to be one of the primary reason for fauna diversity and production of boulder reefs (Wennhage & Pihl 2002, Christie et al. 2009). Thus the macrophyte community that formed after the restoration on Læsø Trindel is most likely the primary reason for the observed increase in invertebrate abundance and biomass.

The restoration also increased the abundance and biomass of especially crustaceans and gastropods which included several grazing species. The crustaceans were dominated by smaller species but larger invertebrates commonly associated with temperate stone reefs such as Brachyura (Dahl et al. 2003) also profited from the new habitat.

Prey associated with hard bottom habitat and vegetation were significantly more numerous in cod stomachs after the restoration suggesting increased prey opportunity. The prey species were mainly the large crustaceans such as squat lobsters (Galatheidae) and fish. These large crustaceans had substituted the small crustaceans (Gammaridae), which the cod almost exclusively fed upon before the restoration. A positive relationship exists between prey abundance and predation rate up to the point of satiation (Breck 1993). Hence, the observed biomass increase in cod stomachs is probably caused by an increase in prey availability on the reef. The vegetation after restoration thus provided a habitat that supports an increase in fauna abundance and hence provides good feeding opportunities for juvenile cod. Models of different reef designs have shown the importance of the vegetation area for an increased prey production where several flat reefs could sustain four times more cod with food compared to a tall reef with the same volume of boulders (Møhlenberg et al. 2016). The restoration project on Læsø Trindel increased both the complexity and the relief. The biomass of perennial macroalgae increased (Stenberg et al. 2015) along with the availability of invertebrates thereby increasing the number of fish the reef could sustain with food.

Although the prey availability increased fivefold after the restoration of the boulder reef, the abundance of prey was still lower than on two similar reefs in the Kattegat area; Hatter Barn and Lillegrund & Mejl Flak (**Table 4**). One could expect that the abundance and biomass of the study site was at least similar to two other reefs near Læsø Trindel with a slightly lower salinity. However, when comparing the results of Stål et al. (2007) to those obtained in the present study, the mean abundance of macrofauna in our study site is comparable to those obtained on soft bottom by Stål et al. (2007) and reflects the poor habitat quality prior to restoration. The restoration of the boulder reef increased the macrofauna density, which is a little higher than the densities shown by Stål et al. (2007) on rocky bottoms. Although the macrofauna densities were lower on the restored boulder reef compared to other Danish reefs, the rocky bottom studied by Stål et al. (2007) might be more comparable to Blue Reef based on proximity (Skagerrak, within 100 km) and the level of exposure. The comparison with Stål et al. (2007) are furthermore relevant as the same sampling techniques were applied, i.e. a “suction sampler with a 1 mm sieve (Thomasson & Tunberg 2005).

It was evident that the ecological succession at Blue Reef was still evolving at the time of the last sampling. It can therefore be expected that future sampling of the study site will show even higher abundances and biomasses at Blue Reef. These results are in alignment with the systems approach theory (Hopkins et al. 2012) that conservation and protection of existing natural reefs would be more sustainable and economical viable than exploitation and subsequent restoration.

Goldsinny and corkwing wrasse were specialized feeders but with similar prey preferences. They shared approximately 80% of the prey species available on Læsø Trindel. Goldsinny wrasse has traditionally been viewed as the wrasse species in need of crevices in the reef (Costello 1991, Sayer et al. 1993) whereas the corkwing wrasse inhabited the vegetation (Quignard & Pras 1986, Lythgoe & Lythgoe 1991). The different microhabitat is often reflected in differences in diet between the two species (Sayer et al. 1996). However, goldsinny territories generally consist of a centrally placed shelter hole with algae making up the boundary at one side of the territory (Hilldén 1981). Goldsinny wrasse can thus easily forage in the vegetation area and this may explain the dietary overlap found in this study.

Cod and saithe shared approximately 40% of the prey species found at Læsø Trindel and the adults of both species were primarily piscivorous. It is known that cod becomes increasingly piscivorous with increasing length (Høines & Bergstad 1999). Few studies have described the ontogenetic dietary changes of saithe and they only demonstrated little or no variation in the diet of adult saithe as their size increase (Høines & Bergstad 1999, Jaworski & Ragnarsson 2006). It is clear from our study that saithe are secondary piscivorous and that the diet switches to fish at ~20 cm. The primary reason for the switch in diet is probably increased energy requirements as the fish grow (Keast 1985) in combination with their pelagic predatory behaviour. Although adult cod and saithe consumed fish the prey species differed. Cod predated in the demersal zone on *Callionymus*, *Labrus*, *Lumpenus lampretaeformis*, *Pholis gunellus*, *Zoarcea viviparus*, pleuronectiformes as well as other cod. Saithe on the other hand preyed on pelagic *Trachurus trachurus* as well as Ammodytidae which are known to form schools when feeding (van Deurs et al. 2011).

As a result of the restoration the reef system changed from a mesopredator-dominated (wrasse) system with ephemeral vegetation to a system dominated by top predators (adult cod, saithe and harbour porpoise) with high abundances of prey associated with vegetation. Overfishing removes top-predators from the marine ecosystems allowing medium-sized mesopredators to control the system (Jackson 2008). Mesopredators such as wrasses and juvenile cod dominated the fish community at Læsø Trindel prior to restoration. After the restoration the carrying capacity increased and Læsø Trindel now supports more fish with food and shelter (Støttrup et al. 2014). Harbor porpoises visited the reef more frequently and stayed for longer periods after the restoration (Mikkelsen et al. 2013). The decline in abundance of mesopredators observed by Støttrup et al. (2014) may be a consequence of increased predation pressure from top predators thus releasing the predation pressure on invertebrates. A similar explanation was put forward by Moy et al. (2008), where mesopredators were believed to be a contributing factor (along with temperature, nutrition, light and substrate) to loss of kelp forests in coastal areas of Norway.

According to the classification of the EU Habitat Directive the Danish boulder reefs are in “unfavourable-bad” ecological condition (Fredshavn et al. 2014). In addition to this, eutrophication, overfishing and global warming push the marine areas towards systems dominated by ephemeral vegetation as a consequence of high predation pressure on invertebrate grazers by mesopredator fish (Worm & Lotze 2006, Jackson 2008, Eriksson et al. 2009, Sieben et al. 2011, Norderhaug et al. 2015). The restoration and stabilization of Læsø Trindel has reversed the effect of these threats as the system is now moving towards more top predators and abundant invertebrates.

Although the reef was in a more stable state after restoration and stabilization of the boulders the succession towards a climax community was still believed to be ongoing four years after restoration in 2012 when the project ended. Studies on the effect of kelp harvest on Norwegian kelp forests showed that although the mobile fauna have potential for quick recolonization, the kelp forest ecosystem do not recover fully for five to seven years (Christie et al. 1998). The results reported in the present study are thus underestimates and further studies at Læsø Trindel will show the full potential of this restoration project. Further studies are needed to clarify whether this restoration approach is viable elsewhere. With a combination of several restored boulder reefs in good ecological condition and a sufficiently large protection zone (MPA) around these reefs and the species occupying the reef, this restoration strategy could potentially help restore or preserve some of the depleted economically important fish stocks. Reef habitats are important feeding areas (Seitz et al. 2014) and habitat loss may affect the populations structure of these species negatively (Sundblad et al. 2014). One of the species that could benefit from this type of restoration projects is the Kattegat cod stock which is at an historically low level and considered outside safe biological limits by ICES since 2000 (ICES 2012) primarily due to overfishing.

Conclusions

The boulder reef restoration increased both the complexity and the area of the reef habitat at Læsø Trindel. The restoration increased the habitat quality of the reef and, as expected, we saw an increase in benthic invertebrates especially in species associated with vegetation and hard bottom habitats. This increase in prey availability was also evident in cod stomach content, where the biomass of prey increased threefold after the reef restoration. Furthermore, a change in diet was observed from smaller crustaceans (Gammaridea) before restoration to prey of higher food quality (Galatheidae, Brachyura and fish) after restoration. The results, thus, confirms the habitat improvements caused by the reef restoration. However, four years after restoring the reef the ecological succession was still in process. Additional studies on Læsø Trindel could show the full potential of this restoration project. The results provide evidence of the potential marine production and ecosystem benefits obtained from restoring destroyed cavernous reefs.

ACKNOWLEDGEMENTS

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REFERENCES

Airoldi L, Beck MW (2007) Loss, status and trends for coastal marine habitats of Europe. In: Gibson R, Atkinson RJA, Gordon JDM (eds) Oceanography and Marine Biology An Annual Review Volume 45. CRC Press, p 345–405

Breck JE (1993) Foraging theory and piscivorous fish: are forage fish just big zooplankton? Trans Am Fish Soc 122:902–911

Carr MH (1994) Effects of Macroalgal Dynamics on Recruitment of a Temperate Reef Fish. Ecology 75:1320–1333

Christie H, Fredriksen S, Rinde E (1998) Regrowth of kelp and colonization of epiphyte and fauna community after kelp trawling at the coast of Norway. Hydrobiologia 376:49–58

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396:221–233

Costello MJ (1991) Review of the biology of wrasse (Labridae: Pisces) in Northern Europe. Prog Underw Sci 16:29–51

Dahl K, Hansen J, Helmig S, Nielsen R, Larsen HS (2001) Naturkvalitet på stenrev. Hvilke indikatorer kan vi bruge? Faglig rapport fra DMU nr. 352.

Dahl K, Lundsteen S, Andersen OGN, Göke C, Rasmussen MB, Stæhr PA, Grønkjær P, Andersen NG, Møhlenberg F (2016) Habitatkvalitet og fødeproduktion. In: Stenberg C, Kristensen LD (eds) Stenrev som gyde- og opvækstområde for fisk. DTU Aqua-rapport nr. 294-2015. DTU Aqua, Institut for Akvatiske Ressourcer, Charlottenlund, p 89–129

Dahl K, Lundsteen S, Helmig SA (2003) Stenrev - havbundens oaser, 1st edn. Danmarks Miljøundersøgelser. Gads Forlag., Copenhagen

Dahl K, Lundsteen S, Tendal OS (2005) Mejlgrund og Lillegrund. En undersøgelse af biologisk diversitet på et lavvandet område med stenrev i Samsø Bælt. Faglig rapport fra DMU nr. 529.

Deurs M van, Behrens JW, Warnar T, Steffensen JF (2011) Primary versus secondary drivers of foraging activity in sandeel schools (Ammodytes tobianus). Mar Biol 158:1781–1789

Eriksson BK, Ljunggren L, Sandström A, Johansson G, Mattila J, Rubach A, Råberg S, Snickars M (2009) Declines in predatory fish promote bloom-forming macroalgae. Ecol Appl 19:1975–1988

Fredshavn J, Søgaard B, Nygaard B, Johansson LS, Wiberg-Larsen P, Dahl K, Sveegaard S, Galatius A, Teilmann J (2014) Bevaringsstatus for naturtyper og arter. Habitatdirektivets artikel 17 rapportering.

Freese L, Auster PJ, Heifetz J, Wing BL (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar Ecol Prog Ser 182:119–126

Gage JD, Roberts JM, Hartley JP, Humphery JD (2005) Potential Impacts of Deep-Sea Trawling on the Benthic Ecosystem along the Northern European Continental Margin: A Review. Am Fish Soc Symp 41:503–517

Gordon JDM (2002) Deep water demersal fisheries. Joint Nature Conservation Committee (JNCC) Available: http://www.jncc.gov.uk/marine/page-2525 (Feb 2016).

Hayward PJ, Ryland JS (Eds) (1995) Handbook of the Marine Fauna of North-Western Europe. Oxford University Press, Oxford

Hilldén N-O (1981) Territoriality and reproductive behaviour in the goldsinny, *Ctenolabrus rupestris* L. Behav Processes 6:207–221

Høines ÅS, Bergstad O a. (1999) Resource sharing among cod, haddock, saithe and pollack on a herring spawning ground. J Fish Biol 55:1233–1257

Hopkins TS, Bailly D, Elmgren R, Glegg G, Sandberg A, Støttrup JG (2012) A systems approach framework for the transition to sustainable development: Potential value based on coastal experiments. Ecol Soc 17:39

ICES (2012) Report of the Baltic Fisheries Assessment Working Group 2012 (WGBFAS). ICES

CM 2012/ACOM:10. 12-19 April 2012. Copenhagen

Jackson JBC (2008) Ecological extinction and evolution in the brave new ocean. Proc Natl Acad Sci U S A 105:11458–11465

Jaworski A, Ragnarsson SÁ (2006) Feeding habits of demersal fish in Icelandic waters: a multivariate approach. ICES J Mar Sci 63:1682–1694

Keast A (1985) The piscivore feeding guild of fishes in small freshwater ecosystems. Environ Biol Fishes 12:119–129

Kirkegaard JB (1992) Danmarks Fauna 83. Havbørsteorme I Errantia. Dansk Naturhistorisk Forening, København

Langton RW (1982) Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish. Fish Bull 80:745–759

Lorentsen SH, Sjøtun K, Grémillet D (2010) Multi-trophic consequences of kelp harvest. Biol Conserv 143:2054–2062

Lythgoe J, Lythgoe G (1991) Fishes of the sea: The North Atlantic and Mediterranean. Blandford, London

Mikkelsen L, Mouritsen KN, Dahl K, Teilmann J, Tougaard J (2013) Re-established stony reef attracts harbour porpoises *Phocoena phocoena*. Mar Ecol Prog Ser 481:239–248

Møhlenberg F, Hansen FT, Uhrenholdt T, Mandviwalla X (2016) Stenrevs placering og udformning. In: Stenberg C, Kristensen LD (eds) Stenrev som gyde- og opvækstområde for fisk. DTU Aqua-rapport nr. 294-2015. Technical University of Denmark, National Institute of Aquatic Resources, Charlottenlund, p 194–233

Mortensen TH (1924) Danmarks Fauna 27. Pighude (Echinodermer). G.E.C. Gads Forlag, København

Moy F, Christie H, Steen H, Stålnacke P, and others (2008) Final report from the sugar kelp project. SFT-rapport TA-2467 2008, NIVA-rapport 5709. Oslo

Norderhaug KM, Christie H, Fosså JH, Fredriksen S (2005) Fish–macrofauna interactions in a kelp (Laminaria hyperborea) forest. J Mar Biol Assoc UK 85:1279

Norderhaug KM, Gundersen H, Pedersen A, Moy F, Green N, Walday M, Gitmark J, Ledang A, Bjerkeng B, Hjermann D, Trannum H (2015) Effects of climate and eutrophication on the diversity of hard bottom communities on the Skagerrak coast 1990-2010. Mar Ecol Prog Ser 530:29–46

Quignard J-P, Pras A (1986) Labridae. In: Whitehead PJ., et al. (eds) Fishes of the northeastern Atlantic and the Mediterranean, Vol. II. UNESCO, Paris, p 919–942

Rossi S (2013) The destruction of the “animal forests” in the oceans: Towards an over-simplification of the benthic ecosystems. Ocean Coast Manag 84:77–85

Sayer MDM, Gibson RRN, Atkinson RJAR (1993) Distribution and density of populations of goldsinny wrasse (Ctenolabrus rupestris) on the west coast of Scotland. J Fish Biol 43:157–167

Sayer M, Gibson RN, Atkinson RJA (1996) Seasonal, sexual and geographical variation in the biology of goldsinny, corkwing and rock cook on the west coast of Scotland. Wrasse Biol Use

Aquac:13 – 46

Schoener TW (1968) The Anolis Lizards of Bimini: Resource Partitioning in a Complex Fauna. Ecology 49:704–726

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological Value of Coastal Habitats for Commercially and Ecologically Important Species. ICES J Mar Sci 71:648–665

Sieben K, Ljunggren L, Bergström U, Eriksson BK (2011) A meso-predator release of stickleback promotes recruitment of macroalgae in the Baltic Sea. J Exp Mar Bio Ecol 397:79–84

Stål J, Pihl L, Wennhage H (2007) Food utilisation by coastal fish assemblages in rocky and soft bottoms on the Swedish west coast: Inference for identification of essential fish habitats. Estuar Coast Shelf Sci 71:593–607

Stenberg C, Støttrup J, Dahl K, Lundsteen S, Göke C, Andersen ON (2015) Ecological benefits from restoring a marine cavernous boulder reef in Kattegat, Denmark. DTU Aqua report no. 289-2015. Copenhagen

Støttrup JG, Stenberg C, Dahl K, Kristensen LD, Richardson K (2014) Restoration of a Temperate Reef: Effects on the Fish Community. Open J Ecol 4:1045–1059

Sundblad G, Bergström U, Sandström A, Eklöv P (2014) Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES J Mar Sci 71:672–680

Tebble N (1966) British Bivalve Seashells. A Handbook for Indentification. British Museum (Natural History), London

Thomasson M a., Tunberg BG (2005) Composition and vertical distribution of the motile epifauna on a vertical rock wall in Gullmarsfjorden, western Sweden, using an alternative sampling approach. Mar Biol Res 1:107–117

Watling L, Norse EA (1998) Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting. Conserv Biol 12:1180–1197

Wennhage H, Pihl L (2002) Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. J Fish Biol 61:207–228

Worm B, Lotze HK (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. Limnol Oceanogr 51:569–579

Table 1. Time of catch and fish length. Fish with empty stomachs are not included here.

	Cod			Saithe	Goldsinny wrasse		Corkwing wrasse
mm	Oct-07	Jun-12	Oct-12	Oct-12	Oct-07	Jun-12	Jun-12
<50							
50					49		5
100	36				20	3	7
150	25	5		33			
200	5	42	9				
250	2	12	11	47			
300	1	2	3	8			
350		4	4				
400			2				
450		2	5				
500		1	3				
550			1				

Table 2. Statistical results of GLM on stomach content of Atlantic cod (*Gadus morhua*)

Taxonomical group	fish leng*BA	fish length	BA
Bivalves	0.905	0.851	0.001 ***
Fish	0.665	0.368	0.060
Gastropods	0.777	0.748	0.728
Malacostraca	0.898	0.029 *	0.055
Gammaridea	<0.0001 ***	<.0001 ***	<0.0001 ***
Pleocyemata	0.204	0.989	<.0001 ***
- Brachyura	0.910	0.798	<.0001 ***
- Caridea	0.404	0.266	0.643
- Galatheidae	0.026 *	0.026 *	<.0001 ***
Multicrustacea	0.757	0.365	0.361
Ostracoda	0.612	0.139	0.181

Table 3a. Stomach content of Atlantic cod (*Gadus morhua*) before and after restoration of a boulder reef. W= Ash free dry weight, F= Frequency

	Oct-07				Jun-12						Oct-12			
	small juveniles < 20 cm		large juveniles 20-35 cm		small juveniles < 20 cm		large juveniles 20-35 cm		adults > 35 cm		large juveniles 20-35 cm		adults > 35 cm	
n	61		8		5		60		7		27		11	
	F%	W%	F%	W%	F%	W%	F%	W%	F%	W%	F%	W%	F%	W%
Malacostraca total	94.3	81.8	90.0	99.5	28.1	100.0	18.0	8.8	33.3	41.0	79.4	84.0	51.1	17.4
Gammaridea	78.9	16.2	10.0	5.1	9.4	2.8	5.9	0.2						
Senticaudata	2.2	5.1					1.6	1.3			26.3	1.9		
Ploecyemata														
Cancridae	1.1	9.1	5.0	7.7			0.2	0.1			3.7	67.4	13.3	17.2
Galatheidae	3.0	29.6			3.1	11.4	0.5	1.1			7.6	2.6	2.2	
Portunoidea	1.0	6.3	20.0	29.5	3.1	0.0	0.1	0.1			8.7	10.6	4.4	0.1
other Pleocyemata	8.1	15.4	55.0	57.1	3.1	77.8	0.7	0.0			10.1	0.6	8.9	0.2
other Malacostraca					9.4	7.9					23.1	1.0	22.2	
Fish total	0.3	0.0			9.4		5.4	88.5	66.7	59.0	5.5	15.3	26.7	82.5
Callionymus ssp.											0.2			
Gadus morhua							0.1				0.2		2.2	
Labrus ssp.							1.4	52.6			0.2			
Lumpenus lampretaeformis									33.3	59.0				
Pholis gunnellus							0.6	35.8					6.7	82.5
Trachurus trachurus													2.2	
Zoarcea viviparus							3.3				0.2			
Perciformes	0.3	0.0			6.3				33.3		4.6	15.3	15.6	
Pleuronectiformes					3.1		0.1							
Bivalves	3.9	0.4	10.0	0.5			0.8	0.0			1.8	0.0	2.2	
Gastropods	0.6	0.2					1.3	0.0			2.1	0.0	2.2	0.0
other	0.8	17.6			62.5		75.2	2.7			11.2	0.6	17.8	

Table 3b. Stomach content of saithe (*Pollachius virens*) after restoration of a boulder reef. W= Ash free dry weight, F= Frequency

	Oct-12			
	small juveniles < 20 cm		large juveniles 20-35 cm	
	F%	W%	F%	W%
n	33		55	
Malacostraca	16.0	62.4	17.0	0.5
Copepods	16.7	0.9	1.0	0.0
Fish			6.6	99.3
Trachurus trachurus			0.9	56.7
Ammodytidae			2.9	39.0
Perciformes			2.9	3.6
Gastropods	49.1	23.5	54.4	0.1
other	18.1	13.1	20.9	0.1

Table 3c. Stomach content of goldsinny wrasse (*Ctenolabrus rupestris*) before and after restoration of a boulder reef. W= Ash free dry weight, F= Frequency

	Oct-07				Jun-12	
	juveniles < 10 cm		adults 10-20 cm		adults 10-20 cm	
	F%	est. W%	F%	est. W%	F%	est. W%
n	49		20		3	
Malacostraca	55.6	73.6	13.7	36.0	8.5	0.4
Gammaridea	50.6	41.6	13.1	29.6		
Senticaudata	3.2	26.4	0.2	6.0	2.9	0.3
Ploecyemata						
Galatheidae	0.1	1.5				
other Pleocyemata	0.9	3.9	0.2			
Fish	0.1					
Gastropods	2.9	0.4	65.6	7.7	71.7	0.3
Bivalves	40.6	10.2	19.8	4.5	2.2	0.0
Other	0.8	15.8	0.9	51.8	11.4	99.2

Table 3d. Stomach content of corkwing wrasse (*Symphodus melops*) after restoration of a boulder reef. W= Ash free dry weight, F= Frequency

	Jun-12			
	juveniles < 15 cm		adults 15-20 cm	
	F%	W%	F%	W%
n	5		7	
Malacostraca			64.4	56.6
Multicrustacea			4.5	0.2
Fish			0.4	0.0
Gastropods			24.2	13.1
Bivalves			0.8	2.0
Other	100.0	100.0	5.7	28.1

Table 4. The availability of fauna on three Danish boulder reefs. ([1]Dahl et al. 2016, [2] Dahl et al. 2005) Salinity data was available from Dahl et al. 2001.

		Average m^{-2}		Total reef		
	Area m^2	Biomass gram AFDW	Abundance No.	Biomass gram AFDW	Abundance No.	Salinity 10 m depth
Blue Reef						
unstable hard bottom	27,000	8	6,722	216,000	181,494,000	28.5
hard bottom	27,000	119	31,534	3,140,890	879,801,848	28.5
Hatter Barn [1]						
hard bottom	129,743	712	95,859	115,455,557	10,214,219,394	20.2
Lillegrund & Mejl Flak[2]						
hard bottom		252	188,414			20.4

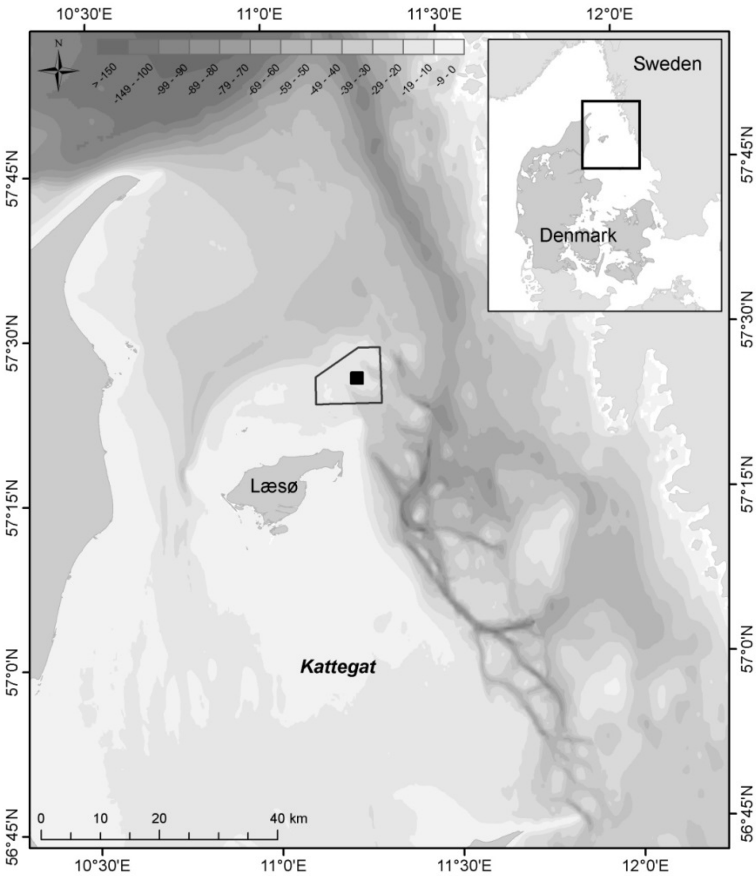

Figure 1. The boulder reef Læsø Trindel (black square) within the NATURA 2000 site no. 168 "Læsø Trindel and Tønneberg Banke" (black outline) in Kattegat between Denmark and Sweden.

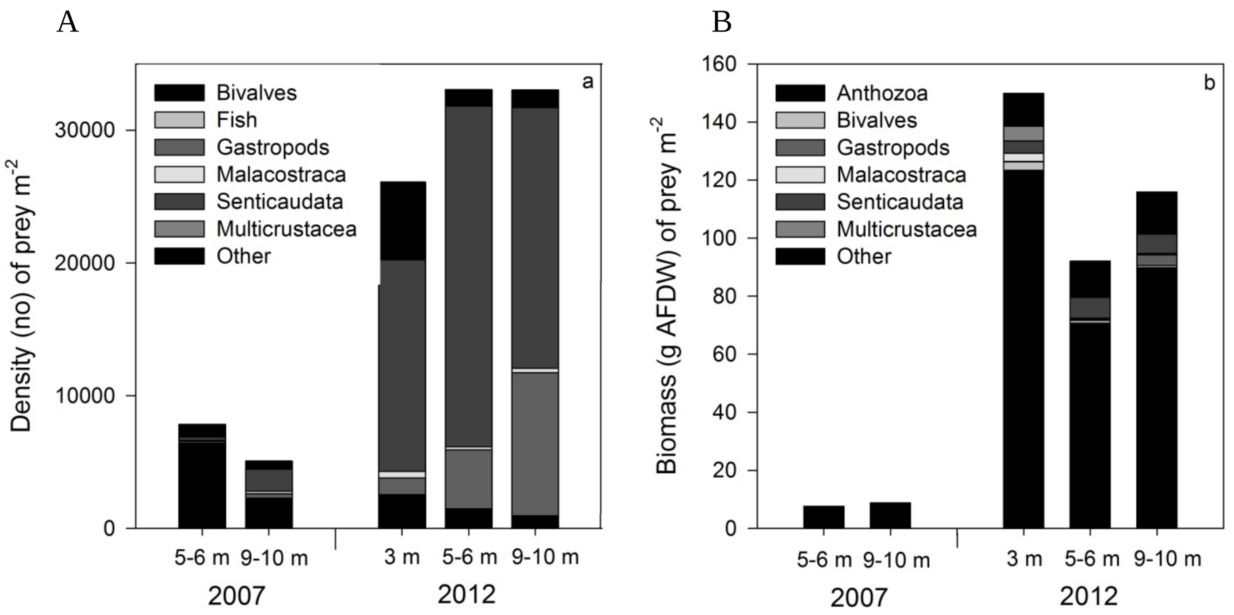

Figure 2. Benthic prey pr. m^2 at three different depths before and after boulder reef restoration. **A** average abundance pr. m^2 and **B** average biomass in Ash Free Dry Weight (ASDW) pr. m^2

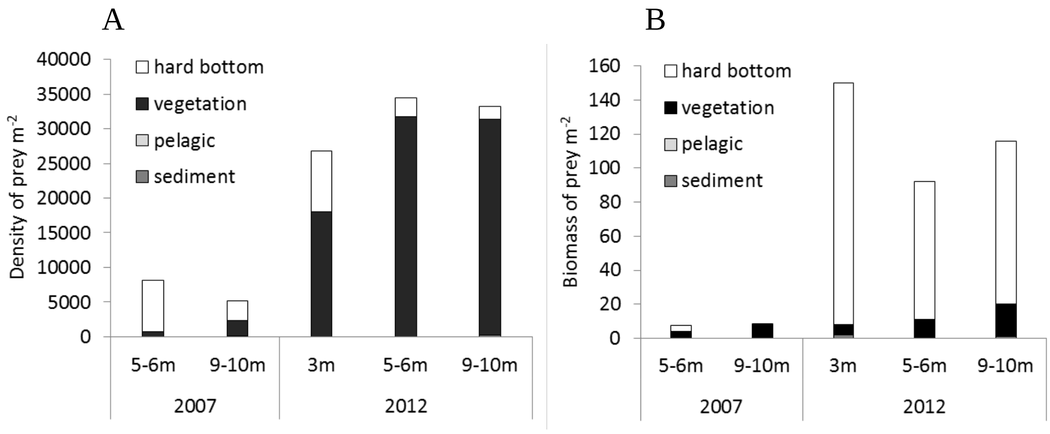

Figure 3. Prey associated with *pelagic*, *sediment*, *vegetation* or *hard bottom habitat* before and after restoration of Blue Reef. A: average abundance of prey pr. m^2. B: average biomass of prey pr. m^2.

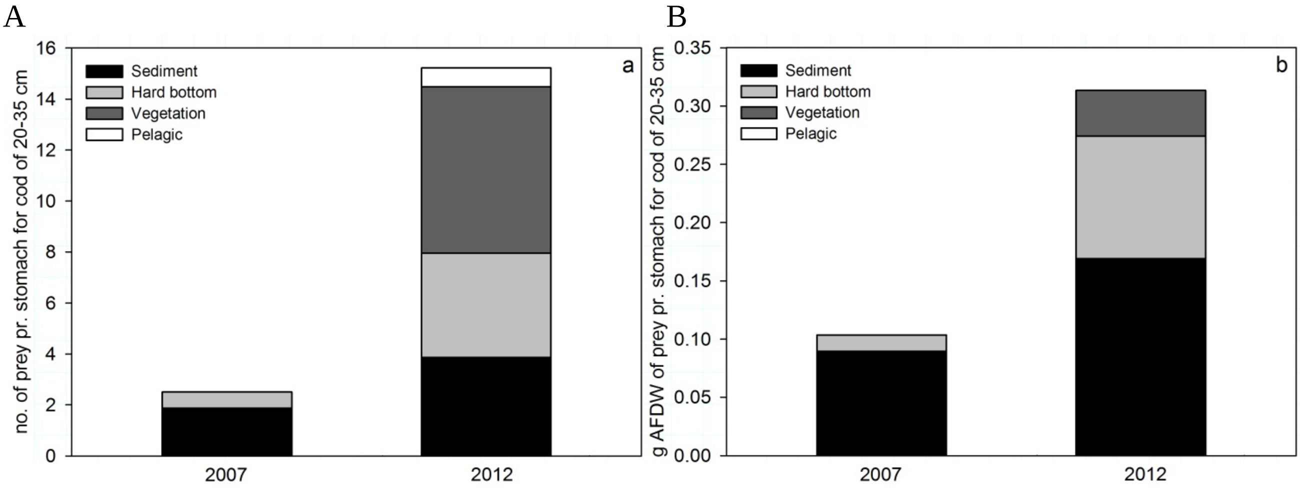

Figure 4. Stomach content of 20-35 cm Atlantic cod (*Gadus morhua*) divided into habitat types *pelagic*, *sediment*, *vegetation* or *hard bottom habitat*. **A**: Average abundance of prey pr. cod. **B**: Average weight (Ash Free Dry Weight) of prey pr. cod.

Paper IV

Behavioural changes of Atlantic cod (*Gadus morhua*) after boulder reef restoration: implications for coastal habitat management

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Manuscript

Behavioural changes of Atlantic cod (*Gadus morhua*) after boulder reef restoration: implications for coastal habitat management

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Abstract Marine reef habitats are degraded globally. The increased awareness of the importance of complex habitats has also increased the focus on restoring them. The responses of fish to reef restoration, particularly in temperate waters, need to be examined as part of the success criteria for reef restoration. Using telemetry, this study measured the effect of boulder reef restoration on the behaviour of Atlantic cod *(Gadus morhua*). Cod were tagged and released in the study area both before and after the boulder reef restoration and tracked continuously for 180 days. A larger fraction of the cod remained in the study area after restoration (94%) compared to before (53%) and they spent more time in the study area after the restoration. These results showed that the function of complex hard bottom substrates can be restored for temperate fish species, associated with complex hard bottom habitats, and may be a viable management tool.

KEYWORDS: reef restoration, Atlantic cod (*Gadus morhua*), marine fish behaviour, management tools, reef degradation, coastal fish habitat.

RUNNING TITLE: Cod behavioural response to reef restoration.

Introduction

Shallow coastal habitats are utilized by 44% of the species that ICES gives advice on in the North Atlantic (Seitz et al. 2014). These shallow coastal habitats, which range from bare sand bottom to complex rocky reefs, constitute important spawning, nursery or feeding areas during one or more fish life stages. Coastal hard substrates, particularly boulder reefs, have high biological production due to the dense macroalgal vegetation attached to the stabile hard surfaces. One kelp algae can hold up to 90,000 individuals from a wide range of species, and in some areas the average fauna density exceeds 500,000 animals pr. m^2 (Christie et al. 2009). The vegetation thus provides good feeding opportunities for several fish species including juvenile Atlantic cod (*Gadus morhua*) (Wennhage & Pihl 2002, Norderhaug et al. 2005). After harvesting a kelp forest, the abundance of juvenile cod may drop by >90% (Lorentsen et al. 2010) confirming the importance of kelp habitats.

Anthropogenic impacts on the coastal marine habitats are a global problem and the impact is especially high in Northwestern Europe, East Asia, North America, the Mediterranean Sea and the East Caribbean due to cumulative effects (Halpern et al. 2008). Among the greatest threats to marine ecosystems are habitat destruction (Lotze et al. 2006) and in Europe it is estimated that 85% of the European coastlines are degraded (Bryant et al. 1995, EEA 1999). Destruction of hard bottom habitats occurs globally as an effect of dredging fisheries e.g. in the UK, Faroe-Shetland Channel and Alaska (Freese et al. 1999, Gordon 2002, Gage et al. 2005) resulting in a reduction in structural complexity (Thrush & Dayton 2002, Gray et al. 2006). Extraction of marine boulders to construct piers, jetties and other coastal constructions took place for at least a century in Denmark peaking in the 1960s and 1970s with a presumed high loss of individuals and species inhabiting the hard bottom habitats (Dahl et al. 2003). Protection of boulder reefs is now in force with the implementation of the European Natura 2000 program. Because of the estimated high loss of this valuable habitat type the first attempt to restore a boulder reef in Denmark was initiated in 2008 (Stenberg et al. 2015).

The cod population in Kattegat Sea between Denmark and Sweden has suffered severe depletion due to overfishing among other things (Cardinale & Svedäng 2004, Frank et al. 2011). The habitat requirements for juvenile cod are fairly understood (e.g. Gregory & Anderson 1997) whereas the habitat requirements for adult cod have received less attention. However, adult cod may utilize vegetated areas to some extent (Wennhage & Pihl 2002, Lorentsen et al. 2010) indicating that benthic vegetation and complex habitats may be important for disparate life stages of cod. A restoration and improvement of the quality of the available benthic habitats could have a positive effect on the threatened cod population (Sundblad et al. 2014).

While the restoration of the boulder reef has revealed promising findings related to benthos, vegetation and mammalian apex predators (Mikkelsen et al. 2013, Støttrup et al. 2014, Kristensen 2016), effects on the behaviour of cod need to be examined. Using telemetry, this study examined the effects of boulder reef restoration on the residence time of Atlantic cod in the study area in the Kattegat Sea. Specifically, we compared the number of tagged cod that remained in the study area one year before restoration (2007) and four years after the restoration (2012). In addition, we determined the number of hours a specific cod was registered per day in the study area throughout a 6-month period (June to December) before and after the boulder reef restoration took place. It was hypothesised that the boulder reef restoration would increase the percentage of cod remaining on the reef and their residence time.

Materials and methods

Study area

The study area was located in the Kattegat Sea between Denmark and Sweden (**Fig. 1**). In the study area, existing reef structures were highly degraded after 100+ years of boulder extraction and were unable to meet the requirements of the EU Habitat Directive (Fredshavn et al. 2014). Therefore, during the summer 2008, a total of 100,000 tons of Norwegian quarry boulders were deposited in the study area covering 27,400m^2. The water depth changed from 5-10 m (mean: 7.6 m) before the deposition of the boulders in 2007 to 3-10 m (mean: 6.6 m) after deposition in 2008 (Stenberg et al. 2015).

Fish capture, tagging and release

Atlantic cod (*Gadus morhua*) (mean 33.5 ± 10.7 cm total length) were captured in the study area using fyke nets in 2007 and 2012. Each fyke net fished overnight (12 h) and cod were taken ashore and tagged on the following day by an experienced fish surgeon according to the method described by Cooke et al. (2003). Each fish was anaesthetized (benzocaine 300 ppm) and equipped with an acoustic transmitter (LP-9; mass: 4 g; length: 23 mm; diameter: 9 mm; 69 kHz; output power level: 142 dB re 1 μ Pa @ 1 m; transmission interval 60-180 s; operation period ≥ 1 year; Thelma Biotel, Trondheim, Norway). Transmitters were inserted through an incision in the body cavity and closed by 2-3 absorbable sutures (Vicryl 5-0FS-2; Ethicon, Piscataway, NJ, USA) following standard procedures (**Fig. 2**) (Svendsen et al. 2011, Piper et al. 2015). Fish total body length was recorded (to nearest 0.5 cm) while anaesthetized. After surgery and recovery (30 min), cod were released at the capture site. Cod were tagged and released in June, both before (2007) and after (2012) the boulder reef restoration. All fish handling procedures were in accordance with the permission 2012-DY-2934-00007 from the Danish Experimental Animal Committee. No fish were sacrificed, all efforts were taken to ameliorate animal suffering and undue stress, and no fish died during the procedures.

Fish tracking and data acquisition

Four acoustic receivers (VR2; 69 kHz; VEMCO Canada) were used as automatic listening stations (ALS) and deployed in the study area before/after. The positions of the ALS before the reef restoration (2007) corresponded to the positions after the boulder reef restoration (2012). On selected ALS a reference transmitter was placed approx. 1 m above the ALS (**Fig. 3**). The ALS with reference transmitter was placed so it could be detected on several neighboring ALS under good conditions. The minimum distance to a neighboring ALS was 200 m. The ALS recorded and stored the individual transmitter codes. If a tagged cod was detected on any of the ALS during a given hour the fish was interpreted as being present in the area during that hour. The number of hours with registration per day (Hours Registered per Day, HRD) per fish was used in the analyses of data. The ALS were in operation for 180 days after each release of tagged fish (i.e. from June to December). The ALS were retrieved by scuba diving. Transmitter detections during the first five days after fish release were disregarded in the data analyses to ensure that tagged fish recovered from the handling and tagging procedures (Heggberget et al. 1988, Svendsen et al. 2004).

Statistical analysis

To account for variability in the detection of the tagged fish we used the information from the reference transmitters. If a reference transmitter was undetected within a distance of 200 m during a given hour all data from that hour was omitted. For a given day, we set a minimum requirement of 6 h with reference transmitter registration for that day to be included in the analysis. There was no difference in diurnal registration of reference transmitter in the study period (ANOVA on number of registration pooled in 6 h interval), $p>0.90$). A relative day factor could therefore be calculated for days with reference transmitter detection between 6 and 23 hours (24/ hour of reference transmitters). This relative day factor was multiplied with the number of hours a tagged cod was registered per day.

The statistical analyses on HRD before/after were carried out in a repeated measurement ANOVA using the proc genmod with a poisson distribution in SAS version 9.4. Fish length was used as covariate. The model was set up with a compound symmetry (type=CS) and repeated within a 14-day period. It was assumed that each consecutive 14-day period was unrelated and could be considered a new event. The estimated HRD from the statistical model was calculated using the least square means (LSMEANS option in SAS) as used for comparison of HRD before/after. The significance level was set at 0.05

Results

The evaluation of detection of reference transmitters indicated a decline in the detection range as the study period progressed (starting in June; data not shown). No diel variation was observed in the average mean detection range of ALS.

In total 33 cod were tagged and released in the study area, divided into 17 released before boulder reef restoration in 2007 and 16 after in 2012. A pronounced difference in post-release behaviour in cod was observed before and after restoration of the boulder reef. Following release, more cod remained in the area in 2012 (94%) compared to 2007 (53%).

The total number of days that fish were observed varied from 1 to 178, where the total study period was 180 days (**Table 1**). Before the restoration of the boulder reef only 1 cod (6%) was observed >50% of the days on the reef. After restoration, a total of 6 (38%) cod was observed >50% of the days on the reef. After the boulder reef restoration, the mean percent-days-observed was 74% among fish observed >50% of the days on the reef. For those fish that was observed <50% of the days on the reef, the mean percent-days was 12%. There was no significant difference between the length of the cod that was observed >50% or <50% of the days on the reef (Student T-test, P=0.36).

The statistical tests showed that there was a significant difference between the mean length of cod that was observed in the study area before restoration (mean TL: 299 ± 66 mm) and those that was never observed on the reef (mean TL: 240 ± 18 mm) (Student T-test, P=0.013). The cod that remained on the reef was significantly larger than those that were beyond the realms of the observed reef area.

There was great variation in the HRD for the individual cod (**Fig. 4**) and the time cod spent in the study area increased significantly after boulder reef restoration (**Fig. 5**). The change in HRD was significant both when comparing the total study period before/after (repeated measurement ANOVA, P<0.0001) and each month separately (cross effect of before/after*month; repeated measurement ANOVA, P<0.0001). The fish length also had a significant effect on HRD (repeated measurement ANOVA, P=0.004).

Discussion

This study demonstrates a change in cod behaviour after the restoration of a boulder reef. After the restoration a larger proportion of cod occupied the reef area and individual cod spent significantly more time on the reef. As no other major ecological changes occurred in the area between 2007 and 2012, the change in cod behaviour observed here is attributed the boulder reef restoration. The positive results presented here indicate that boulder reefs may be an important habitat for maturing or adult cod, and suggest that boulder reef restoration should be a management option in areas where boulder reefs have been severely degraded or destroyed. The boulder reef was restored to meet requirements for the EU Natura 2000 program as reefs represent a distinct nature type under the program. This study shows it is possible to restore a degraded reef habitat with benefits for commercially valuable species such as cod.

The use of animal behaviour in evaluating the quality of restored habitats

Detailed observations of animal behaviour provide valuable information about habitat quality when assessing restoration effects (Lindell 2008, Layman et al. 2014). Restoration projects are usually evaluated based on species presence and richness or enhancement in abundance (Ruiz-Jaen & Aide 2005, Støttrup et al. 2014). Behavioural traits can include fitness consequences as an indicator of habitat quality and may be more cost-efficient (Lindell 2008). This could be done by comparing behaviours of key species before and after restoration rather than documenting the presence/absence of all species (Lindell 2008). According to this definition, cod increased fitness by remaining longer in the study area after restoration of the boulder reef. The conclusion is supported by other studies on the restored reef, where an increase in the biomass and abundance of prey was observed in cod stomachs (Kristensen 2016). Therefore, the use of residence time is, in this case, justified as a behavioural trait with fitness consequences indicating habitat quality after restoration of the boulder reef.

Relocation between suitable habitats are associated with energy costs (Kramer & Chapman 1999), and HRD was thus a suitable behavioural trait to evaluate the habitat quality of the restored reef. For fish, a high quality habitat provides both shelter from predation and an abundance of food items. The increase in biomass of perennial macroalgae on the restored reef (Karsten Dahl, personal observation) improved the quality of the reef habitat, since vegetation is associated with high abundances of invertebrate fauna (Christie et al. 2009) and provides good feeding opportunities for cod (Wennhage & Pihl 2002). Increased prey availability of both invertebrates and fish were observed (Støttrup et al. 2014, Kristensen 2016). The improved habitat quality is reflected in the increased residence time of the individual cod after reef restoration.

Site fidelity

With the boulder reef restoration, the fraction of cod remaining on the reef >50% of the days in the study period and thereby demonstrating high site fidelity (Lindholm & Auster 2003) increased from 6% to 38%. Interestingly, other studies have observed similar patterns with approximately one-third of tagged cod exhibiting high site fidelity (Lindholm & Auster 2003, Lindholm et al. 2007). Thus, individual cod may exhibit different dispersal strategies, with some individuals exhibiting high site fidelity while other individuals tend to disperse over much larger distances. Previous studies have suggested that individual dispersal strategies depend on physiological states (Brodersen et al. 2008, Poulsen et al. 2010, Boel et al. 2014) and variation in individual boldness (Chapman et al. 2011). Our data add to these findings by indicating that dispersal strategies in cod may depend on the quality of the available habitat. Additional studies may reveal whether the effect of habitat availability on dispersal is induced by the habitat changing the physiological state (e.g. starvation) of the individual fish. High site fidelity was to be expected on deep boulder reefs (50-100 m depth) or wrecks that in a topographic context generally are isolated within a homogenous low-relief seafloor (Lindholm et al. 2007, Karlsen 2011). In such isolated areas, feed excursions will probably increase energy demands as well as the predation risk. It is thus surprising that a highly mobile species such as cod would demonstrate this degree of site fidelity in a shallow area with other reefs in the vicinity. It could suggest that after restoration the boulder reef now constitutes a habitat of high quality for cod. The quality of the surrounding reefs is unknown but could be investigated through further studies. Another explanation for the high site fidelity is that the utilization of resources is more efficient when the fish is familiar with the area and a change of home range is often associated with energy costs (Kramer and Chapman 1999). It is thus interesting to note that even though it was associated with a higher energy cost, many of the tagged cod were absent throughout the study period before reef restoration. Diver observations (Karsten Dahl, personal observation) confirmed that prior to restoration the reef was unstable and the pebbles/gravel scoured off the vegetation only allowing fast-growing ephemeral algae to persist. The habitat quality of the study area prior to restoration was thus so inferior that the benefits of changing home range was greater than the net benefits of staying.

Utilization of the boulder reef

Physical structures have a positive influence on juvenile cod growth and population size (reviewed by Lilley & Unsworth 2014). Strong evidence suggests that juvenile cod use structures including highly productive vegetation (Christie et al. 2009) both for foraging (Lorentsen et al. 2010) and to seek shelter from predators. Juvenile cod hide in cobble or vegetation to reduce predation risk when exposed to an actively foraging older conspecific (Gotceitas & Brown 1993, Gotceitas et al. 1995, 1997). Prior to the restoration, only the larger cod were registered in the study area, suggesting limited habitat suitability for small cod due to either limited prey availability or lack of shelter from predators. According to a previous study on the restored reef (Kristensen 2016), the smallest size classes of cod (20-35cm) mainly depended on crustaceans (84%) whereas the larger size classes (35-55cm) were piscivorous (82%). Although the two largest, tagged fish only spent a few days on the restored reef, there was no significant difference in the size of cod that spent > or < 50% of the days on the reef. This implies that the restored reef was not only a good quality habitat providing feeding opportunities for the small crustacean-eating cod but also for the larger and maturing piscivorous cod.

For cod, as in many other species, there is a trade-off between feeding and the risk of predation. In the presence of poor quality habitats cod (30-60 cm) foraged on low quality prey items instead of undertaking energetically demanding food excursions in search for high quality prey with increased predation risk (Kaspersen 2008). Also Lindholm & Auster (2003) found unexpected high site fidelity for 38-60 cm cod in gravel – a substrate often preferred by far smaller cod. Before the restoration, only larger cod were observed and site fidelity was low indicating either poor feeding opportunity or high predation risk provided by the unstable boulder reef. After the restoration, the increased structural complexity provided more shelter opportunity increasing the abundance of cod and their site fidelity (this study) as well as a broader size range of cod (Støttrup et al. 2014). Furthermore, the restored boulder reef resulted in elevated presence of large predators such as saithe (*Pollachius virens*) and harbor porpoise (*Phocoena phocoena*) (Mikkelsen et al. 2013, Støttrup et al. 2014).

Management perspectives

The full extent of the damages caused by the removal of boulders for the construction industry is unknown. The size of available nursery areas influences the population size of marine species (Sundblad et al. 2014), and it remains unknown to what extent the extraction of boulders in Danish waters have had on the Kattegat cod population. The results presented here suggest that habitat restoration and the addition of structural complexity to the benthic environment may revert the damages at least to some degree.

The reduction of food and shelter availability may have increased the vulnerability of cod to predators but possibly also to fishery, as most fishing occurs in less heterogeneous substrate to prevent gear loss (Watling & Norse 1998). Future studies should investigate the importance of other marine habitats such as gravel and sand habitats affected by extraction activities and dredging fisheries for marine organisms. This knowledge is important for management of MPAs or marine spatial planning (MSP). Furthermore, understanding the spatial dynamics of marine species is important to develop further management strategies, such as “no-take”-zones or for MSP, to support sustainable fishery.

Conclusions

To our knowledge, this is the first study quantifying fish behaviours in relation to temperate reef restoration. The results demonstrate that a larger fraction of the tagged cod remained in the study area after the boulder reef was restored (93%) compared to before (53%). Moreover, throughout the study period, cod continuously spent more time in the study area after the restoration. Our study indicated that the restored boulder reef improved habitat for cod through increased food availability and shelter from predators. We recommend boulder reef restoration as a valuable management tool to improve habitats for temperate fish species that are associated with complex hard bottom habitats.

Acknowledgements

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References

Boel M, Aarestrup K, Baktoft H, Larsen T, Søndergaard Madsen S, Malte H, Skov C, Svendsen JC, Koed A (2014) The physiological basis of the migration continuum in brown trout (*Salmo trutta*). Physiol Biochem Zool 87:334–345

Brodersen J, Nilsson PA, Hansson L-A, Skov C, Brönmark C (2008) Condition-dependent individual decision-making determines cyprinid partial migration. Ecology 89:1195–1200

Bryant D, Rodenburg E, Cox T, Nielsen D (1995) Coastlines at risk: an index of potential development-related threats to coastal ecosystems. WRI Indic Br (World Resour Institute, Washington, DC)

Cardinale M, Svedäng H (2004) Modelling recruitment and abundance of Atlantic cod, *Gadus morhua*, in the eastern Skagerrak-Kattegat (North Sea): Evidence of severe depletion due to a prolonged period of high fishing pressure. Fish Res 69:263–282

Chapman BB, Hulthén K, Blomqvist DR, Hansson LA, Nilsson J-Å, Brodersen J, Nilsson PA, Skov C, Brönmark C (2011) To boldly go: Individual differences in boldness influence migratory tendency. Ecol Lett 14:871–876

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396:221–233

Cooke SJ, Graeb BDS, Suski CD, Ostrand KG (2003) Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: case study of a novice and experienced fish surgeon. J Fish Biol 62:1366–1380

Dahl K, Lundsteen S, Helmig SA (2003) Stenrev - havbundens oaser, 1st edn. Danmarks Miljøundersøgelser. Gads Forlag., Copenhagen

EEA (1999) Environment in the European Union at the turn of the century. State of Environment Report, 1/1999. Copenhagen

Frank KT, Petrie B, Fisher JA, Leggett WC (2011) Transient dynamics of an altered large marine ecosystem. Nature 477:86–89

Fredshavn J, Søgaard B, Nygaard B, Johansson LS, Wiberg-Larsen P, Dahl K, Sveegaard S, Galatius A, Teilmann J (2014) Bevaringsstatus for naturtyper og arter. Habitatdirektivets artikel 17 rapportering.

Freese L, Auster PJ, Heifetz J, Wing BL (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. Mar Ecol Prog Ser 182:119–126

Gage JD, Roberts JM, Hartley JP, Humphery JD (2005) Potential Impacts of Deep-Sea Trawling on the Benthic Ecosystem along the Northern European Continental Margin: A Review. Am Fish Soc Symp 41:503–517

Gordon JDM (2002) Deep water demersal fisheries. Joint Nature Conservation Committee (JNCC) Available: http://www.jncc.gov.uk/marine/page-2525 (Feb 2016).

Gotceitas V, Brown J (1993) Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93:31–37

Gotceitas V, Fraser S, Brown J a. (1995) Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Mar Biol 123:421–430

Gotceitas V, Fraser S, Brown JA (1997) Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 54:1306–1319

Gray JS, Dayton P, Thrush S, Kaiser MJ (2006) On effects of trawling, benthos and sampling design. Mar Pollut Bull 52:840–843

Gregory RS, Anderson JT (1997) Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Mar Ecol Prog Ser 146:9–20

Halpern BS, Walbridge S, Selkoe KA, Kappel C V., Micheli F, D’Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A Global Map of Human Impact on Marine Ecosystems. Science (80-) 319:948–952

Heggberget TG, Hansen LP, Næsje TF (1988) Within-river spawning migration of Atlantic Salmon (*Salmo salar*). Can J Fish Aquat Sci 45:1691–1698

Karlsen JD (2011) Hot on the tail of hefty Atlantic cod: an interdisciplinary study on the behaviour at ship wrecks in the North Sea. Aarhus University

Kaspersen M (2008) Torskens (*Gadus morhua*) fouragering på forskellige habitater i Nordsøen. University of Southern Denmark

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. Environ Biol Fishes 55:65–79

Kristensen LD (2016) The importance of habitat structure for the distribution and behaviour of demersal fish. Technical Univeristy of Denmark

Layman CA, Jud ZR, Arrington A, Sabin D (2014) Using Fish Behavior to Assess Habitat Quality of a Restored Oyster Reef. Ecol Restor:140–143

Lilley RJ, Unsworth RKF (2014) Atlantic Cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. Glob Ecol Conserv 2:367–377

Lindell CA (2008) The Value of Animal Behavior in Evaluations of Restoration Success. Restor Ecol 16:197–203

Lindholm J, Auster P (2003) Site utilization by cod in off-shore gravel habitat. Mar Technol Soc J 37:27–34

Lindholm J, Auster PJ, Knight A (2007) Site fidelity and movement of adult Atlantic *cod Gadus morhua* at deep boulder reefs in the western Gulf of Maine, USA. Mar Ecol Prog Ser 342:239–247

Lorentsen SH, Sjøtun K, Grémillet D (2010) Multi-trophic consequences of kelp harvest. Biol Conserv 143:2054–2062

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–9

Mikkelsen L, Mouritsen KN, Dahl K, Teilmann J, Tougaard J (2013) Re-established stony reef attracts harbour porpoises *Phocoena phocoena*. Mar Ecol Prog Ser 481:239–248

Norderhaug KM, Christie H, Fosså JH, Fredriksen S (2005) Fish–macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. J Mar Biol Assoc UK 85:1279

Piper AT, Svendsen JC, Wright RM, Kemp PS (2015) Movement patterns of seaward migrating European eel (*Anguilla anguilla*) at a complex of riverine barriers: Implications for conservation. Ecol Freshw Fish:1–12

Poulsen SB, Svendsen JC, Jensen LF, Schulz C, Jäger-Kleinicke T, Schwarten H (2010) Effects of food deprivation on refuge use and dispersal in juvenile North Sea houting *Coregonus oxyrinchus* under experimental conditions. J Fish Biol 77:1702–1708

Ruiz-Jaen MC, Aide TM (2005) Restoration success: How is it being measured? Restor Ecol 13:569–577

Seitz RD, Wennhage H, Bergström U, Lipcius RN, Ysebaert T (2014) Ecological Value of Coastal

Habitats for Commercially and Ecologically Important Species. ICES J Mar Sci 71:648–665

Stenberg C, Støttrup J, Dahl K, Lundsteen S, Göke C, Andersen ON (2015) Ecological benefits from restoring a marine cavernous boulder reef in Kattegat, Denmark. DTU Aqua report no. 289-2015. Copenhagen

Støttrup JG, Stenberg C, Dahl K, Kristensen LD, Richardson K (2014) Restoration of a Temperate Reef: Effects on the Fish Community. Open J Ecol 4:1045–1059

Sundblad G, Bergström U, Sandström A, Eklöv P (2014) Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES J Mar Sci 71:672–680

Svendsen JC, Aarestrup K, Malte H, Thygesen UH, Baktoft H, Koed A, Deacon MG, Cubitt KF, Mckinley RS (2011) Linking individual behaviour and migration success in Salmo salar smolts approaching a water withdrawal site: implications for management. Aquat Living Resour 24:201–209

Svendsen JC, Koed A, Aarestrup K (2004) Factors influencing the spawning migration of female anadromous brown trout. J Fish Biol 64:528–540

Thrush SF, Dayton PK (2002) Disturbance to Marine Benthic Habitats by Trawling and Dredging: Implications for Marine Biodiversity. Annu Rev Ecol Syst 33:449–473

Watling L, Norse EA (1998) Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting. Conserv Biol 12:1180–1197

Wennhage H, Pihl L (2002) Fish feeding guilds in shallow rocky and soft bottom areas on the Swedish west coast. J Fish Biol 61:207–228

Figure captions

Figure 1. The study area (indicated with the black square) within the Natura 2000 site in the Kattegat Sea between Denmark and Sweden.

Figure 2. Standard procedures for insertion of acoustic transmitter into the body cavity of Atlantic cod (*Gadus morhua*). The incision was closed by three sutures. Cod were captured using fyke netting and released at the same location after operative recovery.

Figure 3. Mooring of hydrophones in the marine environment. Each hydrophone constituted an automatic listening station (ALS) in the study area.

Figure 4. The mean estimated residence time in Hours Registered per Day (HRD) and percentage estimated for each individual Atlantic cod (*Gadus morhua*) per week in the study period (180 days). a) registrations before and b) after boulder reef restoration. The temperate boulder reef was restored in 2008.

Figure 5. The mean estimated residence time in Hours Registered per Day (HRD) for Atlantic cod (*Gadus morhua*) for each complete month in the study area before (2007) and after (2012) boulder reef restoration. The temperate boulder reef was restored in 2008.

Figures:

Figure 1.

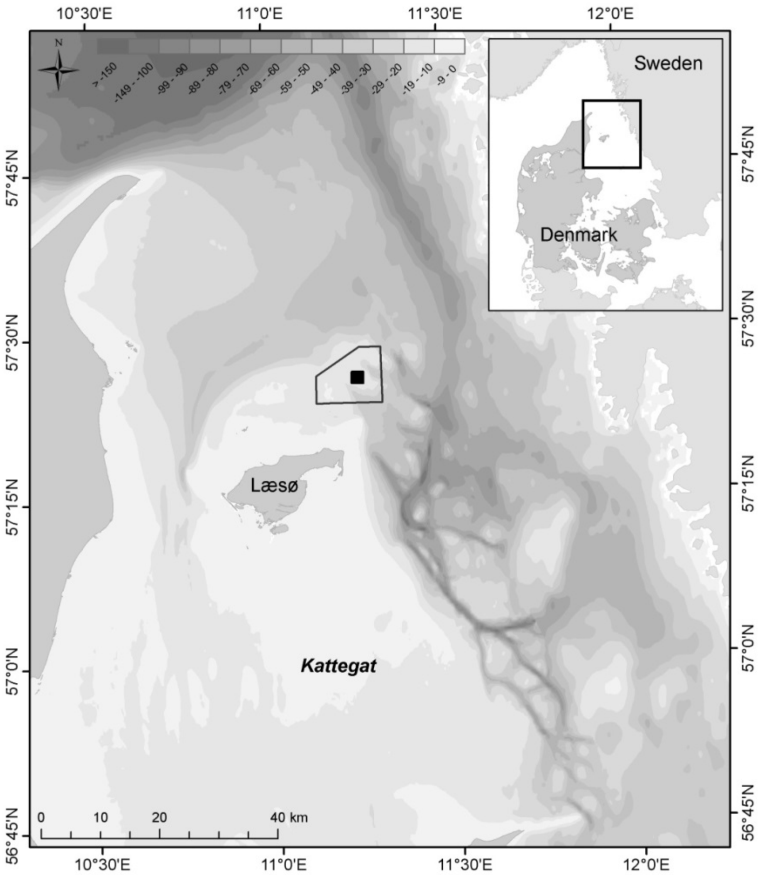

Figure 2.

Figure 3.

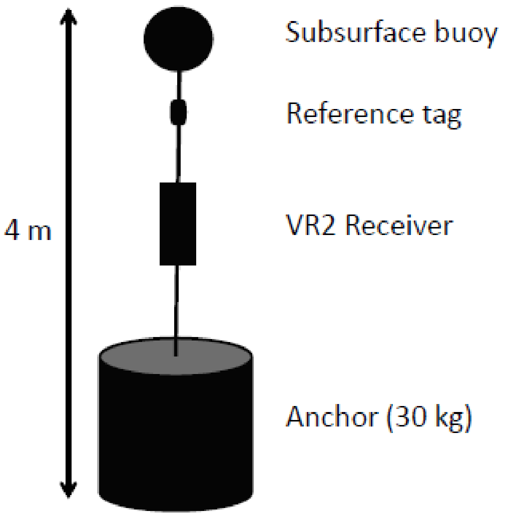

Figure 4.

a) b)

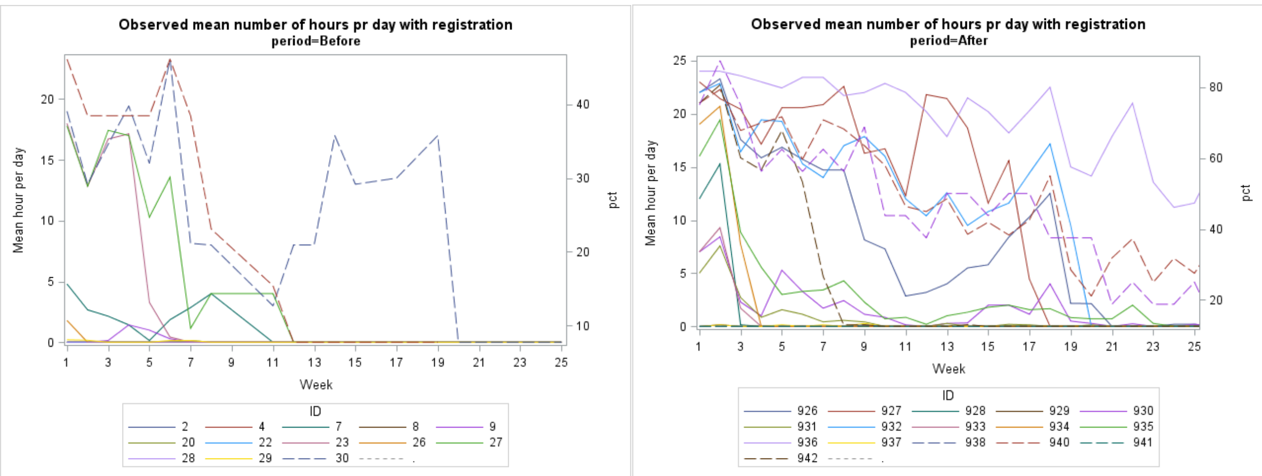

Figure 5.

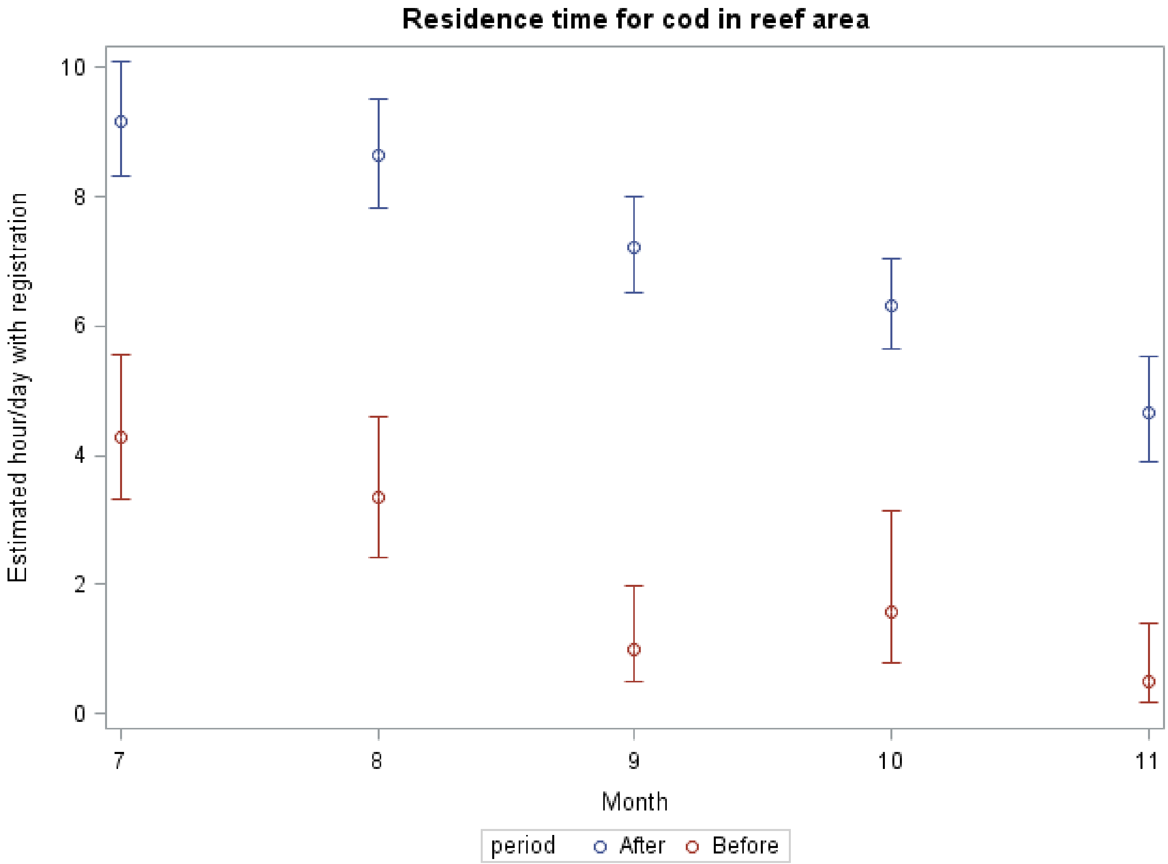
Residence time for cod in reef area
Estimated hour/day with registration
0
2
4
6
8
10
7
8
9
10
11
Month
period
After
Before

Table 1. Summary of data for 33 Atlantic cod (*Gadus morhua*) tagged with acoustic transmitter and released in the study area before (2007) and after (2012) boulder reef restoration. The temperate boulder reef was restored in 2008. TL=Total length.

Before				After			
ID	**TL (mm)**	**Total number days observed**	**% days observed**	**ID**	**TL (mm)**	**Total number days observed**	**% days observed**
2	260	1	1	926	340	124	69
3	240			927	350	116	64
4	205	1	1	928	350	17	9
5	235			929	410	3	2
6	235			930	410	79	44
7	435	35	19	931	540	39	22
8	240			932	360	136	76
9	325	9	5	933	420	19	11
19	240			934	350	23	13
20	250	1	1	935	480	100	56
22	365	1	1	936	450	180	100
23	230	38	21	937	700	11	6
26	260	3	2	938	270	1	1
27	270	57	32	940	350	165	92
28	265			941	410	1	1
29	255	4	2	942	230	50	28
30	300	122	68				
Mean	**271**		**9**	**Mean**	**401**		**37**
Sum		**272**		**Sum**		**1064**	

This PhD project investigated the effects of coastal habitat structural characteristics on the biodiversity, abundance, size range and behaviour of fish, whilst maintaining a particular focus on the effect of habitat restoration. Unique results are presented from established blue mussel (*Mytilus edulis*) beds and the first ever restored boulder reef. The results are thus highly relevant for future management of degraded hard bottom habitats. This PhD thesis indicates that establishment of blue mussel beds and boulder reef restoration could be a valuable management tool to improve habitats for temperate fish species.

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